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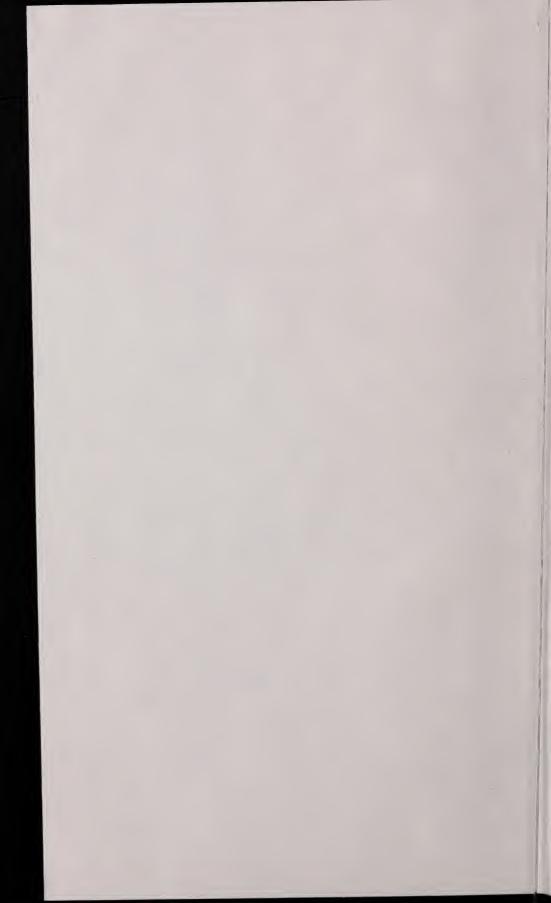
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# Hidden Genetic Variation in Agraulis vanillae incarnata (Nymphalidae)

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Abstract. Two culture lines of Agraulis vanillae incarnata were established from one wild-collected female. One line was mass selected for reduced black markings, the other for increased black markings. Both lines were maintained through seven generations, at which time the phenotypic differences between the lines diverged in response to selection; a scale deformity also occurred among some individuals in the lightly marked culture. Some genetic aspects of the variation discovered are discussed.

#### Introduction

The purpose of the present work was to determine if any genes for albinic, melanic, or immaculate Agraulis vanillae incarnata (Riley) were carried by a field collected gravid female. These variants occur rarely in nature, and have been described as aberrants "hewlettii" Gunder (1930), "comstocki" Gunder (1925), "margineapertus" Gunder (1928), and "fumosus" Gunder (1927). The probability of randomly selecting a specimen carrying such gene(s) is admittedly small, and when it became obvious that simple single gene variants were not likely to be expressed in culture, the breeding program was modified to ascertain whether extreme opposite phenotypes could be produced in parallel cultures through mass selection. Since the color and pattern of A. vanillae throughout its range in southern California is quite constant, this program would provide information on the amount of hidden genetic variation in the taxon. In A. vanillae, which is orange with black markings on the upperside, the approach involved selecting adults toward an all-orange upperside in one culture line and an all-black upperside in the other. A final goal was to cross the selected lines in order to test whether the resulting hybrids would restore the normal phenotype, as might be expected in a complex polygenic system (Lerner, 1954, 1958). Although the original project never reached completion, the results obtained after seven generations are of sufficient interest to be presented here.

## Mating and Rearing Protocol

The original female was collected on 29 October 1982 in Ventura, California. She was confined for oviposition in a flight cage 51 x 51 x 122 cm with several water-potted cuttings of the larval foodplant *Passiflora caerulea*. The cage received afternoon sunshine plus light from a 75-watt GE Gro and Sho Spotlight after sunset. Although courtship and mating in this species occurs throughout the day in warm weather in natural conditions, in this indoor breeding program these activities were limited to the latter half of the day when the flight cage received more light.

Smaller cages for mating single pairs of adults were made from cardboard boxes measuring 23 x 32 x 32 cm. The top and sides were cut out, nylon netting glued over these sides, and a door cut out from the margin of one side. When a specific pair had been chosen and mating required confirmation, the caged butterflies were left in a warm room with ambient light until noon, when they were taken out to a car. When placed on the front seat in sunlight (or occasionally on bright but overcast skies), and with an inside temperature of 24-30°C, matings almost always occurred. Opening one or both car windows to provide a slight breeze helped stimulate mating.

Ovipositing females and their progeny were left in these small cages. Cut *P. caerulea* in water lasts up to two weeks, so new cuttings were added as the older ones began to decline or were consumed, and the larvae eventually found their way onto the new plants. The large flight cage was also used as a rearing cage for broods of up to 800 larvae.

During the last instars it was necessary to clean out the denuded vine stems and frass twice weekly. It was important to keep an adequate supply of foodplants readily available for the larvae, as they cannibalized pupae if these were discovered before foodplant. When most or all larvae had pupated, the cage was cleaned and twigs with prepupae or pupae were cropped to c. 8 cm and pushed into styrofoam mounted on a cardboard base. Eclosing adults were examined for characteristics desired for breeding and placed into appropriate cages. Less extreme phenotypes were saved as papered specimens. All others were liberated.

Under the above conditions, the average time for one life cycle was 45 days. Thus the entire breeding schedule described here required  $10\frac{1}{2}$  months.

## The Breeding Program

A pedigree of the breeding program is shown in Figure 1. Except for those instances where a single pair of adults was mated and their offspring reared separately, the majority of the culture lines involved several mixed pairs representing an extreme selected phenotype. Thus the term **mass selection** is used, as multiple individuals were involved in most crosses. The number varied in each generation, but was usually limited to the five

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or ten lightest or darkest pairs. When more extreme phenotypes occurred late in the broods, their earlier less extreme counterparts and their ova were discarded or moved to a general mass rearing cage.

Adults from broods 1, 2, 4 and 7 showed no significant variation from typical phenotypes. One-third of the pupae of brood 6 blackened and died, and the remainder discarded. Many adults in brood 5 were unable to fly properly, suggesting viability modifiers. They fluttered upside down on the cage floor and so were not used for breeding, with the exception of a dark female (2(5)DAD) which was mated to a slightly dark male from the mixed brood 2mix. No  $G_3$  or  $G_4$  descendants from this mating expressed the flight affliction. One female (3D/S DAD female #3) from the  $G_3$  of this line showed reduced silver on the hindwing underside and was mated to a male (3D/S D) from the dark culture (results below). The 3D/S D male was mated to two other females.

The hindwing upperside marginal chain pattern tended to break on the discal side in brood BB, a characteristic we call "broken bridges". This line was inbred until the  $G_3$  adults were obtained (Figs. 41-42), then abandoned due to lack of space.

### **Extreme Light and Dark Lines**

Brood 8 was the major source of lightly marked adults used for selecting the "immaculate" phenotype. This line was maintained through the seventh generation. By the seventh generation, the upperside black spots in the forewing interspaces  $M_3$ ,  $Cu_1$ ,  $Cu_2$  and hindwing interspaces RS,  $M_3$  and at the base of RS- $M_1$ , were entirely absent in most specimens. The forewing marginal triangles and the hindwing marginal chain markings were also greatly reduced. However, the forewing discal cell markings did not respond to selection and remained normal in size. The gradual development of this phenotype is shown in Figures 2-16. The results suggest that different genes or sets of genes independently control these two sets of markings.

A selection of dark adults from the mixed brood was the source of specimens for the dark phenotype. The remainder of specimens from the mixed brood and those from brood 3 were discarded. After four generations they did not exhibit facies as dark as the  $G_2$  dark mixed brood. From this  $G_2$  brood, the darkest specimens (3DD) were bred for one generation. Then, in the  $G_4$ , offspring from the  $G_3$  female 3DD female #2 and  $G_3$  male 3D/S D were included in this brood. The dark line was then inbred until the  $G_7$  adults eclosed. The development of this phenotype is shown in Figures 17-28. (This line shares with the "immaculate" line the  $P_1$  female and  $G_1$  adults in Figures 2-4.)

## Variation in Undersurface Silvering

The 3D/S D male (Fig. 37), which mated three times, displayed reduction in the silver maculation on the hindwing underside. Development of

the silver markings was never a consideration in the selection of the light and dark phenotypes, but the presence of two females with similar reductions in silver markings presented an opportunity to breed this variation. When the female 3D/S D female #1 (Fig. 38) was mated to this male, offspring were as follows: 36 normal males, 52 normal females, one male with slight silver reduction, and three females with moderate silver reduction. When the same male was mated to female 3D/S DAD female #3 (Fig. 40), which also displayed reduced silver markings, the offspring (26 males and 20 females) were all silvered normally. The same male was mated to a normally silvered dark female, 3DD female #2 (Fig. 39), and their offspring (35 males and 49 females) were also all silvered. Finally, from a mixed brood of several pairs of adults with reduced silver markings, the following offspring were obtained: 53 normal males, 58 normal females, and two males and four females with reduced silver markings. The partially unsilvered condition exhibited by several adults was usually not displayed by their offspring, thus the heritability of the character will remain in doubt until further controlled experiments can be performed.

Comparison of the silver markings of the G<sub>7</sub> light phenotypes (Figs. 29-30) with those of the dark phenotypes (Figs. 31-32) show differences in development, especially with the "slipper-shaped" silver spot in interspace RS on the hindwing. In the light phenotype the two halves of this spot nearly coalesce; in the dark phenotype the halves have become widely

separated and smaller.

## Greasy-wing

A variation having a scale deformity occurred in about 12 individuals of the  $G_5$  generation of the "immaculate" line. These variants were called "greasy-winged" (GW) because of their resemblance to specimens with wings smeared by body fluids. This scale deformity affected all scales, including those on the body. Examples of the deformity are shown together with scales from a normal specimen in the scanning electron microscope photographs in Figures 43-48.

The SEM photographs show that in wild type individuals the pigmented scales differ in shape from silver scales (Fig. 42). At the highest magnifications, the pigmented scales show spaces between the ribs, while the silver scales in the inter-rib area appear solid. In GW individuals all scales are reduced in size and are narrower. Further, the ultrastructure (Figs. 45 & 48) is modified such that the inter-rib area of all scale types appears partially filled or plugged. The effect is apparently a breakdown of the diffractive properties of the scale surface, producing partial transparency.

The source of GW variants was the pooled brood of 4imm adults. This brood consisted of ca. 10-15 pairs of normal adults, and their pooled G<sub>5</sub> offspring consisted of ca. 100 normal "immaculate" phenotypes and ca. 12 GW adults (the 5GW and 6GW lines were established from these). None of 25(1):1-14, 1986

these "greasy-wings" was as extreme as those which occurred in later broads. However, extreme "greasy-wings" did result from matings between normal "immaculate"  $G_6$  adults.

The results of further crosses of the 4imm line to show inheritance of GW follow:

### G<sub>4</sub> offspring 100 normal:12 GW

	Normal x Normal	GW x GW
$G_5$	(pair)	(mass mating)
Normal male	12	2
Normal female	10	0
GW male	9	64
GW female	7	66

# From above, Normal x Normal

$G_6$	(pair)
Normal male	19
Normal female	23
GW male	17
GW female	7

Extreme GW examples are illustrated in Figures 33 & 36. The transparency of the wings is indicated by the striped paper placed under the wings of the specimen in Figure 34.

Data from both  $G_5$  and  $G_6$  pairings indicate the character is autosomal and probably digenic, resulting from the interaction of paired non-linked complementary genes. Thus a cross of two heterozygote wild types would be expected to produce a 9+:7 GW ratio. The pooled data give a better fit  $(X^2 = 1.4, df = 1, p > .25)$  to 9:7 than to the 3:1 ratio for a single recessive  $(X^2 = 10.1, df = 1, p < .001)$ . Further, if GW were due to a simple recessive, the phenotype should have appeared in the  $G_2$  or  $G_3$  generations.

The "greasy-wing" scale deformity probably decreases fitness, and would appear to be strongly selected against in nature. Meconium discharged from eclosing adults was not repelled by individuals with the GW wings, but rather stuck to them and dried, sometimes causing wings to stick together. Other specimens had lesions on the wings which oozed body fluids at the time of wing expansion. Individuals that were able to expand their wings successfully behaved normally; but because of the non-repellent nature of their wings, they would most likely experience difficulty in humid or rainy conditions.

The cultures were terminated at the end of August 1983 for two reasons. First, the abandoned orchard which had become completely overgrown with *Passiflora caerulea* was cleared for development, eliminating the foodplant resource, and an artificial diet was not further available. Second, TED developed a bronchial irritation from constant exposure to the culture, which was maintained in his living quarters.

#### Discussion

The exploratory work reported here clearly shows that a significant amount of potential genetic variation was present but masked in a single mated female of a phenotypically constant butterfly. The variants produced during the course of seven generations of inbreeding and selection included individuals with substantially greater or lesser quantities of melanin than typical A. vanillae, individuals with the scale anomaly greasy-wings, and individuals with behavioral modifications. The genetic systems producing these effects range from what appears to be complexes of polygenes controlling general wing pattern density to a digenic mendelian pair of genes for greasy-wings. Little research on inbreeding and mass selection has been reported in the Lepidoptera (Robinson, 1971), although inbreeding and selection is a widely used technique to determine the amount of genetic variation in organisms (Lerner, 1954, 1958; Lewontin, 1974). However, note Oliver's, 1981, work on inbreeding depression and some early work by Schrader, 1911. Oliver (1981) showed genetic variability in terms of lethal equivalents in 12 lepidopteran species.

To the extent that the mated female tested is representative (a subsequent abbreviated three generation experiment involving another female produced both light and dark trending individuals, as well as the "broken bridges" phenotypes) one might ask: why are such variants not observed more frequently in nature? Two named aberrants "comstocki" and "margineapertus" occasionally turn up in collections. These aberrations closely resemble the extreme dark and light individuals selected in this breeding program. Our results imply the genetic control of wing melanin is not based on a few simple mendelian genes at the simultaneous recovery of both "comstocki" and "margineapertus" types from a single individual would be quite unlikely given the rarity of these aberrants in nature. An albino aberrant "hewlettii" occurs very rarely in nature. The "greasywing" trait, reported above, has not been reported previously. The data reported here lead us to conclude that substantial heterozygosity for wing character variants exist in natural populations of A. vanillae.

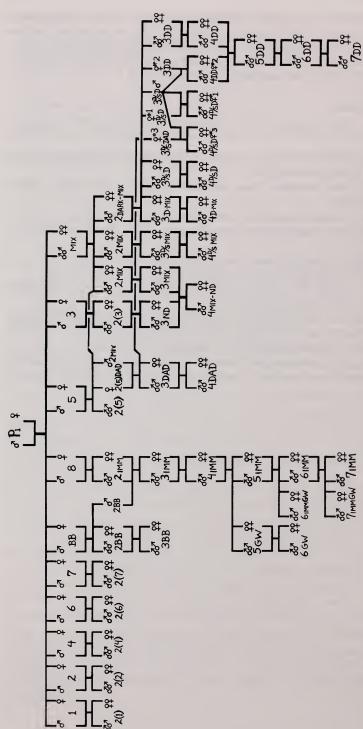
The magnitude of genetic variation we extracted from a single mated individual has implications to both conservation and systematics. In conservation the increasing use of captive breeding programs cannot over emphasize the necessity of attempting to utilize a selective and breeding scheme which maintains wild type individuals, while sequestering variance. In systematics, the results are interesting as applied to butterflies, since butterfly taxonomy at both species and subspecies levels is based largely on wing character states which involve minor changes. The range of variants mass selected from our single female could well represent several different subspecies, if not species, if found fixed in natural populations.

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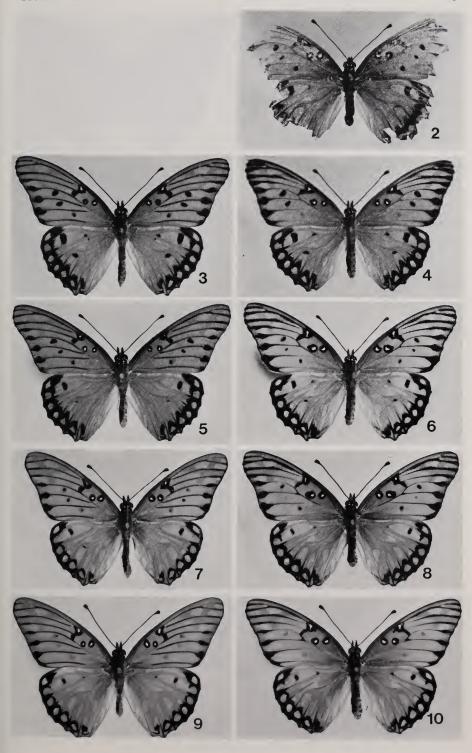
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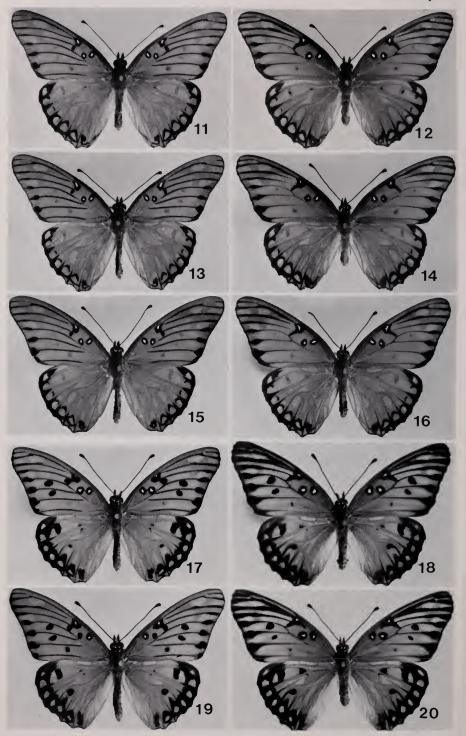
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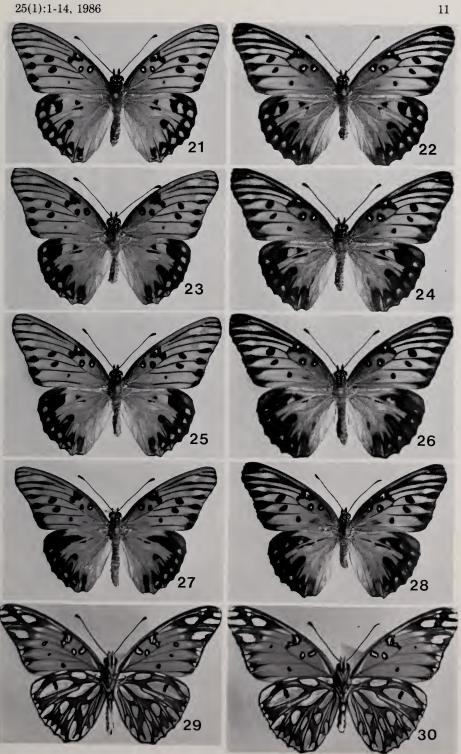


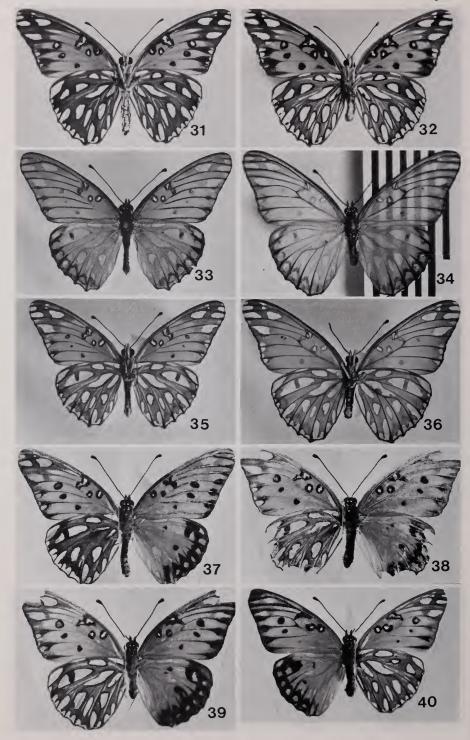
Pedigree of mass selection breeding project using Agraulis vanillae incarnata. Single sex symbols indicate one pair of adults were mated to obtain progeny; double sex symbols indicate two or more pairs of adults. Numbers indicate filial generation. Abbreviations: BB Broken Bridges; D Dark; DAD Dark and Disabled; DD Darkest Darks; D/S Diminished Silver; GW Greasy-winged; IMM immaculate phenotype; MIX Large number of randomly mated individuals; ND Next Darkest Fig. 1.

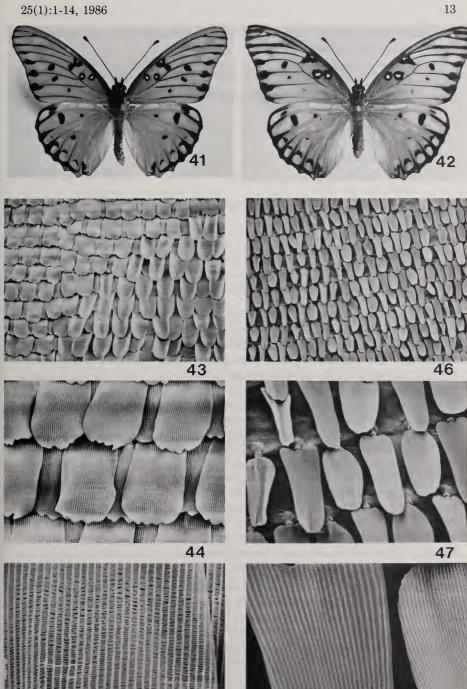
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Selectively bred adults of *Agraulis vanillae incarnata*. Males on left, females on right, except where noted otherwise.

Fig. 2. wild P<sub>1</sub> female.

Figs. 3, 4. G<sub>1</sub>.

Adults bred for reduced black markings ("immaculate" phenotype):

Figs. 5, 6: G<sub>2</sub>; Figs. 7, 8: G<sub>3</sub>;

Figs. 9, 10:  $G_{\Delta}$ ;

Figs. 11, 12: G

Figs. 13, 14: G<sub>6</sub>;

Figs. 15, 16: G<sub>7</sub>.

Adults bred for increased black markings (dark phenotype):

Figs. 17, 18: G<sub>2</sub>;

Figs. 19, 20: G<sub>2</sub>

Figs. 21, 22: G<sub>4</sub>;

Figs. 23, 24: G<sub>5</sub>

Figs. 25, 26: G<sub>6</sub>;

Figs. 27, 28: G<sub>7</sub>.

Figs. 29, 30: Undersides of "immaculate" phenotypes in Figs. 15 and 16.

Figs. 31, 32: Undersides of dark phenotypes in Figs. 27 and 28.

Figs. 33, 34: "Greasy-winged" scale deformity. Male  $F_6$ , female  $F_7$ .

Figs. 35, 36: Undersides of Figs. 33 and 34.

Fig. 37. G<sub>3</sub> male 3D/S. Left side ventral.

Fig. 38. G<sub>3</sub> female 3D/S Df#1. Left side ventral.

Fig. 39. G<sub>3</sub> female 3DD\$#2. Left side ventral.

Fig. 40.  $G_3$  female 3D/S D $\sharp$ #3. Right side ventral.

Figs. 41, 42. G<sub>3</sub> "broken bridges" phenotype.

Fig. 43. Scanning electron microscope photograph of the wing underside of a normal female, brood 7imm. Magnification 160 X. Dark brown scales at upper left, silver scales at lower right.

Fig. 44. Same as Fig. 43, magnification 640 X, dark brown scales.

Fig. 45. Same as Fig. 43, magnification 2500 X.

Fig. 46. Wing underside of a "greasy-winged" female, brood 7immGW. Magnification 160 X. Dark brown scales.

Fig. 47. Same as Fig. 46, magnification 640 X.

Fig. 48. Same as Fig. 46, magnification 2500 X.

Note: The photographs of the adult butterflies were all shot at f5.6 at 1/250th of a second exposure. Varying developing exposures by the automated commercial processing equipment has resulted in photographs in which the orange ground color of the butterflies appears to vary in brightness, which in reality is not the case. Both males and females of the "immaculate" phenotype are consistently bright orange. Dark phenotype males are slightly deeper orange, and their females are auburn-orange.

# Electrophoretic Evidence for Speciation within the Nominal Species Anthocharis sara Lucas (Pieridae)

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**Abstract.** The taxa *Anthocharis sara* and *A. stella* in northern California are shown to be differentiated at the species level, using electrophoretic genetics of both allopatric and parapatric populations. Both are also strongly differentiated from a sample of Colorado *A. julia*.

#### Introduction

Taxonomists confronted with sets of apparently closely-related, allopatric entities are usually forced to decide on purely morphological grounds whether to call them species or subspecies. Occasionally their judgment can be put to test when genetic information becomes available on the entities in question. Since the discovery of sibling speciation, it has been generally recognized that there is no a priori correlation of morphological differentiation and barriers to gene flow. The outcome of such genetic tests, thus, is frequently surprising.

Anthocharis sara was described by Lucas in 1852, presumably from somewhere near San Francisco, California. Its "subspecies" of current usage, stella W. H. Edwards, 1879 and julia W. H. Edwards, 1872, were described from Nevada (type locality restricted to Marlette Peak, Carson Range, Washoe Co., by F. M. Brown, 1973) and Colorado (type locality restricted by Brown, loc. cit., to Beaver Creek, Park Co.). The present study of the A. sara complex was undertaken when one of us (AMS) observed an unusual pattern of interaction in the geographic distributions of the northern California taxa—a pattern which suggested that sara sara and sara "stella" might in fact be full species.

Anthocharis sara sara is distributed in the Central and North Coast Ranges, the Yolla Bollys, the Siskiyou Mountains (including the Trinity Alps), the Cascades north of Mount Shasta, the Sierra Nevada foothills and lower montane zone on the west slope, and in Sierra Valley on the east slope at 1500m, 40 km N of Truckee. In northern California outside the Sierras, it reaches at least 2000m. On the Sierran west slope, AMS has done regular sampling at a series of stations in the South Yuba river country since 1972. At the lowest of these, Washington (803m), only sara sara

has been seen. At Lang Crossing (1500m) neither sara nor stella appears to be a permanent resident, but both have been taken with about equal frequency and no sign of intergradation. At Donner Pass (2100m), stella is a permanent resident and sara has been recorded three times; at Castle Peak (2750m) sara was seen twice. At Truckee (ca. 1800m), on the east slope, only stella occurs. That sara occasionally intrudes at Donner Pass was noted by Emmel and Emmel (1962, p.30), who wrote that "males identical to typical white reakirtii were occasionally taken in fresh condition" ("reakirtii" Edwards being a spring form of sara). The suspicious components of this distribution are: i) the replacement of stella by nominate sara at high altitudes outside the Sierra; ii) the fluctuating altitudinal range at Sierran mid-elevations, without apparent intergradation (Table 1); and iii) the close juxtaposition of stella with nominate sara north of Truckee, in an apparent Great Basin habitat (juniper woodland and meadows with a characteristic Basin butterfly fauna). We therefore decided to seek electrophoretic evidence bearing on the probability of gene flow and the degree of genetic differentiation among accessible populations. Colorado A. "sara" julia was brought into the study as an independent geographic comparison because a sample was available; we had no predictions concerning its status.

#### Materials and Methods

Samples were collected as listed in Table 2; California localities are shown in Fig. 1. All animals were transported alive and immediately stored at -70°C until electrophoresis. Only 1984 and 1985 catches were used.

The head and thorax of each individual were homogenized in 4 volumes of Tris-HCl buffer (0.05 M, pH 8.0). Horizontal starch gel electrophoresis was used, following slightly modified standard procedures (Ayala et. al., 1972; Geiger, 1981). Twenty enzymes were scored: adenylate kinase (loci AK-1 and AK-2), aldolase (ALD), arginine kinase (APK), fumarase (FUM), glutamate-oxaloacetate transaminase (GOT-1, GOT-2), glutamate-pyruvate transaminase (GPT), glyceraldehyde-phosphate dehydrogenase (GAPDH),  $\alpha$ -glycerophosphate dehydrogenase ( $\alpha$ -GPDH), indophenol oxidase (IPO), isocitrate dehydrogenase (IDH-1, IDH-2), malate dehydrogenase (MDH-1, MDH-2), malic enzyme (ME-1), phosphoglucomutase (PGM), 6-phospho-gluconate dehydrogenase (6-PGD), phosphoglucose isomerase (PGI), and pyruvate kinase (PK).

The genetic interpretation of the zymograms is based on the analysis of the progeny of parents with various phenotypes at each polymorphic locus in *Pieris brassicae* (L.) (Geiger, 1982). No deviation from the pattern observed in *P. brassicae* has been found in any of the three taxa investigated here. However, there is some evidence for sex-linked inheritance of the very weakly polymorphic 6-PGD in *stella* (no polymorphism has been detected in female *sara* or *julia*). As this is quite speculative, it has been neglected in the calculations of allelic frequencies; this treatment does not affect any of the conclusions of this paper.

The designation of the alleles indicates the difference in the mobility of the enzyme relative to the most frequent electromorph found in *P. brassicae* (index 100). An allele 95, then, codes for an enzyme that migrates 5 mm less than the *P.* 

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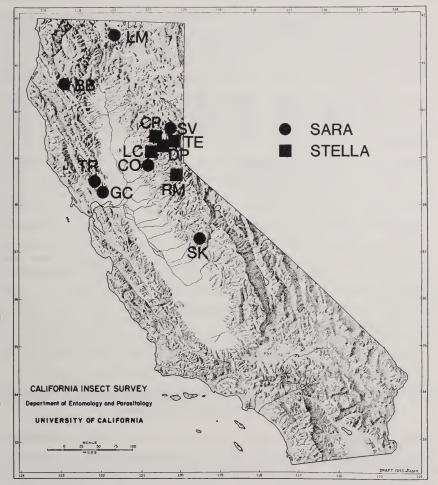


Fig. 1. Localities of *Anthocharis* samples studied. Abbreviations as in Table 2.

brassicae variant.

The allelic frequencies (Tables 3 and 4) have been used to calculate the statistic  $\overline{I}$  (Nei, 1972). These values have then been used to construct a dendrogram (Fig. 2) by cluster analysis (UPGMA method, see Ferguson, 1980).

#### Results

The same electromorphs (treated as alleles) occur in all individuals of all three taxa at nine of the 20 loci investigated (AK-1, AK-2, ALD, APK, FUM, GPT, GADPH, IPO, IDH-2). At four other loci (GOT-2,  $\alpha$ -GPDH, 6-PGD, PK) very infrequent polymorphism is observed (frequency of the common allele >95%, with the exception of the Donner Pass sample (stella) at the 6-PGD locus, f<sub>common allele</sub> = 85%). All samples of all three taxa share the same common allele for these loci. Variation within and/or

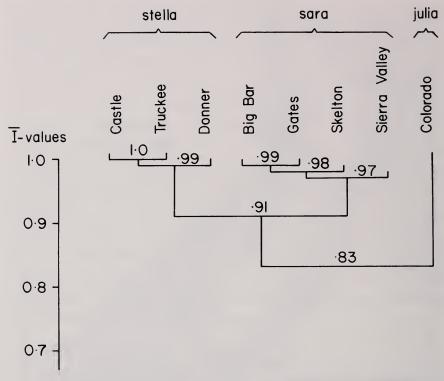


Fig. 2. Dendrogram representing degree of relationship among *Anthocharis* populations for which large samples are available.

between the three taxa was found at seven loci (GOT-1, IDH-1, MDH-1, MDH-2, ME-1, PGM, PGI). The allelic frequencies at these loci are presented in Tables 3 and 4 for all samples with at least five individuals and for pooled samples of the three taxa. At three loci (GOT-1, MDH-1, PGI) most alleles detected in sara with frequencies >10% are also found in stella (Table 3). The two taxa show only small differences in the allelic frequencies at these three loci. This is also true for the observed variation within the two taxa, with the exception of the Sierra Valley sample of sara. In this sample the allele 98 is the common allele at GOT-1, with a frequency of 67% (Table 3). Only a very low level of polymorphism is recorded in our julia sample at these three loci. The common alleles reach very high frequencies but appear identical with the common alleles in sara and stella.

The situation is different at four other loci (IDH-1, MDH-2, ME-1, PGM) (Table 4). Statistically significant differences occur at all four loci among the three taxa (P<1%). The IDH-1 allele 72 is found at 97% in sara and 100% in julia but only 3% in stella. The common allele in stella at the IDH-1 locus is the allele 82 that is found at 3% in sara but not in julia. At the MDH-2 locus the allele 91 is monomorphic in all sara and stella sam-

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ples, but an allele 94 is monomorphic in julia. Sara and stella share the same polymorphism at the ME-1 locus and in both taxa, allele 100 is the common allele. The allele 103 that reaches 19% in sara and 9% in stella is the common allele in julia, with a frequency of 100%. At the PGM locus, alleles 97, 103 and 111 are observed with frequencies >5% in sara. Only allele 97 occurs in julia, and only at very low frequency. The three most common alleles in stella (90, 105, 113) are not recorded in sara and julia at all. The common allele in julia (88) is found at low frequency in sara, and not at all in stella.

These data show a low degree of differentiation within the taxa, even over substantial distances and in different climatic regimes (sara), but a much higher degree between taxa. The quantified data are presented as I-values in a dendogram (Fig. 2). Overall genetic differences within stella are small (I-values  $\geq 0.99$ ). A very similar degree of divergence occurs between the sara samples, despite their wider geographic separation. Within sara, near-coast samples are more similar to one another than to Sierran ones (Skelton Canyon, west slope; Sierra Valley, east), as would be predicted. All the within-taxa comparisons are similar to values obtained within other Pierid taxa at morphospecies level (Geiger,1981; Geiger and Scholl, 1982a, 1982b, 1985). The genetic differences between the taxa are much more pronounced, and similar to those observed between morphospecies of Pieridae (references as above).

The degree of heterozygosity is remarkably low in *julia* ( $H_{\rm obs.}$ =0.028,  $H_{\rm exp.}$ =0.019). The values for sara ( $H_{\rm obs.}$ =0.091,  $H_{\rm exp.}$ =0.117) and stella ( $H_{\rm obs.}$ =0.107,  $H_{\rm exp.}$ =0.120) are clearly higher.

#### Discussion

Low genetic differences among local populations within sara and stella are good indicators of either contemporary or recent gene flow. The situation is very different when these two taxa are compared, even over short geographic distances. The Sierra Valley population of sara, which is 40 km north of the Truckee stella population (and only about 14 km from the nearest known stella, at Yuba Pass), is somewhat different from other sara samples but not in any way that suggests any gene exchange with stella; to the contrary. At two loci (IDH-1, PGM; Table 4) the two taxa only very infrequently have the same alleles in common, and at PGM the commonest allele in each taxon is completely unknown in the other. These are unambiguous indicators of a lack of gene flow between the taxa. As Table 1 shows, the opportunity for contact exists at least in the South Yuba River country and probably elsewhere. We have never, however, found any specimen intermediate between sara and stella either in the wild or in collections, nor do we know of any permanent population (as contrasted with the Lang Crossing case) in which both coexist.

Are sara and stella distinct species, then? In the absence of breeding-compatibility data such a claim may seem premature, but their level of

genetic differentiation is quite normal for Pierid morphospecies; to put it another way, the decision to rank them as subspecies rather than species has been based on a perceived low level of morphological differentiation, which may not be commensurate with genomic differentiation. They are kept apart by a narrow elevational band at mid-elevations on the Sierran west slope in which both may colonize but neither appears capable of permanent establishment. That this band is not "simply" a consequence of habitat selection is shown by the fact that sara replaces stella in very similar habitats and plant associations at high elevations in the Trinity Alps (Shapiro, Palm, and Wcislo, 1981) and the Cascades north of Mount Shasta (Ball Mountain). The nature of the exclusion from mid-elevations on the west slope needs further study. It is duplicated with remarkable precision in at least two other difficult groups: Phyciodes pratensis Behr/montana Behr (Nymphalidae) and Polites sabuleti Bdv./tecumseh Grinnell (Hesperiidae).

The genetic differences are even more pronounced between sara/stella and Colorado julia. This julia population possesses an MDH-2 allele so far unknown in the other taxa; at the PGM locus it shares a common polymorphism with sara but with a different common allele. Given the wide range of the taxon julia (Wyoming to New Mexico) and the complex variability of the sara complex in the Rocky Mountains and Great Basin, it is certainly premature to say too much—except that, on the face of things, julia looks genetically like a well-defined morphospecies.

The average heterozygosity for sara and stella is typical for Pierid species (Geiger, unpublished data) and only a little lower than for invertebrate species in general (H=0.134; Ayala, 1984). Julia is extraordinarily homozygous, however. This could be due to sampling error (n=9), although this value seems not to be affected by similar or even smaller numbers in our sara and stella samples (e.g., sara, Big Bar, n=5,  $H_{obs.}$ 0.124; stella, Castle Peak, n=11,  $H_{obs.}$ =0.102). If the low value (H<sub>obs</sub> = 0.028) is not a sampling artifact, it could be due to (i) recent origin of the species, (ii) a recent bottleneck for either the species or the local populations, (iii) founder effect, (iv) low effective population size, (v) strong selection, or some combination of these and other factors. These matters cannot be resolved until more information is obtained on the genetic structure of julia populations from different parts of its range. This, in turn, is a prerequisite for determining its precise taxonomic standing vis-a-vis not only sara and stella but the six other named entities of the sara complex. At the same time, re-examination of the morphological characters in the complex and the criteria for weighting seems in order, as do compatibility experiments and a careful comparison of both the standard and micromorphology of the early stages.

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- Table 1. Records of **Anthocharis sara sara** and **A. "sara" stella** in the South Yuba River country, northern Sierra Nevada, 1972-1985.
- Washington, Nevada Co., 803 m: sara sara only, uncommon.
- Lang Crossing, Nevada Co., 1500 m: sara sara: 29.iv.74, 15.vi.74, 18.v.75, 15.vi.78; "sara" stella: 2.vi.74, 9.vi.75, 17.iv.77, 6-8.v.84, 19.v.84.
- Donner Pass, Placer-Nevada Cos., 2100 m: sara sara: 2.vii.75, 15.vi.77, 13.vii.77; "sara" stella abundant all years.
- Castle Peak, Nevada Co., 2750 m: sara sara: 30.vi.72, 8.vii.77; "sara" stella all years, scarce to abundant.

Table 2. Samples of the **Anthocharis sara** complex used in this study. Abbreviations are as in Fig. 1.

#### California sara sara:

Trinity-Siskiyou Mountains: Trinity County, Big Bar (BB), Hwy. 299, 37 km W Weaverville, 475 m, 5.v.1985 (n=5).

North Coast Ranges: Napa County: Turtle Rock (TR), Hwy. 128 near Lake Berryessa, serpentine, 160 m, 17.iii.1984 (n=1). Solano County: Gates Canyon (GC), Vaca Hills above Vacaville, 250-500 m, 20.iii.1984 (n=9), 4.iv.1985 (n=3).

Cascade Range: Siskiyou County: Little Shasta Meadow (LM), jct. USFS roads 47N03 and 40N09, Ball Mountain, 2000 m, 12.vi.1985 (n=3).

East Slope Sierra Nevada: Sierra County: Sierra Valley (SV), Hwy. 49, 4 km NE Sierraville, 8.v.1984 (n=6).

West Slope Sierra Nevada: Mariposa County: Skelton Canyon (SK), 1200 m, 9.v.1984 (n=6). Eldorado County: 7 km S Coloma (CO), 300 m, 11.v.1984 (n=1).

#### California "sara" stella:

West Slope Sierra Nevada: Nevada County: vic. Lang Crossing (LC), USFS road 18N18 at South Yuba River, 1500 m, 8.v.1984 (n=2). Nevada + Placer Counties: Donner Pass (DP), Hwy. 40, 2100 m, 27.v.1984 (n=3), 6.vi.1985 (n=10).

Crest, Sierra Nevada: Nevada County: Castle Peak (CP), 2700 m, 6.vi.1984 (n=10), 25.vii.1985 (n=1). Eldorado County: Red Lake Mountain (RM), Carson Pass, 3000 m, 29.vi.1985 (n=1).

East Slope Sierra Nevada: Nevada County: Truckee (TE), 1700 m, 8.v.1984 (n=17).

## Colorado"sara" julia:

Grand County: Willow Creek Cyn., 3.vii.1984 (n=9).

Table 3. Loci with low variability within and between the taxa. n = number of animals investigated

					E			_	MDH-1	-				PGI				
					-105	,			11011	,		ł			-	}	ŀ	T
		c	88	93	96	98 1	105 115	1 79	89	100	81	89	91	97 10	102 10	106 1	115 1	127
sara	Big Bar	5		.30		. 10	09.		06.	.10		.20	.10	.70				
	Gates Canyon	12		.17	80.	•	.71 .04		.88	.13	.04	.25		.54	•	.17		
	Sierra Valley	9				.67	.33		1.0			.33		.58			•	80.
	Skelton	9			-08	•	.92		.92	.08		.25		. 67	80.			
	All samples	34		.10	60.	.13	.66 0.02		.93	.07	.02	.26	.02	. 59	.03	.07		.02
stella	stella Donner Pass	13			.23	. 19	.58		1.0			.42		-19		.35	.04	
	Castle Peak	11			.14	.27	.59		1.0			.36		.36	``	.27		
	Truckee	17	.03		60.	.41	.47	90.	.91	.03	.03	.27		.47	•••	.24		
	All samples	77	.01		.15	.32	.52	.03	96.	.01	.01	.36		.35		. 26	.01	
julia		6					1.0		.94	90.		90.		.94				

Table 4. Loci with high variability within and between the taxa.

n = number of animals investigated

				IDH-1		NDH-2	2	ME-1					Ь	PGM				
		Ľ	72	82	90	91		100	103	88	90	97	103 1	105 10	106 1	111 113	3 120	0
sara	Big Bar	5	1.0			1.0		- 06	.10			.50	07.			.10		
	Gates Canyon	12	96.	.04		1.0		.79	.21	.04		.17	94.	•	.04	.25	.04	7
	Sierra Valley	9	1.0			1.0		1.0		80.			.58			.33		
	Skelton	9	1.0			1.0		.42	.58			.08	.75			.17		
	All samples	34	.97	.03		1.0		.81	.19	.04		.15	.53	•	.02	.25	.02	2
stella	stella Donner Pass	13		96.	.04	1.0		.81	.19		.15	.04		.54		.27	7	
	Castle Peak	11	.04	96.		1.0		96.	•04		.18			89.		.14	7	
	Truckee	17	.03	.91	90.	1.0		76.	90.		.12			.77	.03	60.	6	
	All samples	77	.03	.93	.04	1.0	-	.91	60.		.15	.02		.67	.01	.15	5	
julia		6	1.0				1.0		1.0	.83			.17					

# Genetic Differentiation Between Subspecies of Euphydryas phaeton (Nymphalidae: Nymphalinae)

A. Thomas Vawter<sup>1</sup> and Janet Wright<sup>2</sup>

#### Introduction

The checkerspot butterfly Euphydryas phaeton inhabits eastern North America from the maritime provinces of Canada south to Georgia and west to Missouri (Masters, 1968; Bauer, 1975). It is the only species of the genus that occurs in this region, and thus, represents a biogeographic pattern different from that of its congeners in the west, which have ranges that are generally overlapping and in some cases of limited extent. Although E. phaeton is clearly distinct from the western species and does not show the extreme phenotypic variation that some of them do, two subspecies have been described. Euphydryas phaeton phaeton (Drury) occurs in the northern portion of the species' range where it typically inhabits marshy meadows and similar moist habitats favored by its larval foodplant Chelone glabra (Scrophulariaceae); E. p. ozarkae (Masters) occurs to the south and southwest and favors drier upland forested habitats where it reportedly feeds on Gerardia (= Aureolaria: Scrophulariaceae) (Masters, 1968). Bauer (1975) reports that E. p. ozarkae feeds on Lonicera and that larvae from eggs deposited on Lonicera die when transferred to Chelone, and those from Chelone die when placed on Lonicera. He suggests that this larval foodplant intolerance be used as a basis for dividing the taxa. D. Bowers (personal communication) feels Bauer (1975) is in error; she reports that E. p. ozarkae feeds naturally on Gerardia spp., although both it and E. p. phaeton will accept Lonicera and survive on it. Furthermore, E. p. phaeton can be reared equally well on Gerardia or Chelone, but E. p. ozarkae does significantly better on Gerardia. Gerardia-feeding populations apparently also occur in upland habitats in some areas of New York state (Shapiro, 1975).

Although these two recognizable groups of populations are most often treated as subspecies, the marked ecological differences between them and the apparent overlap in their geographic ranges suggests the possibility that they may be sibling species.

Here we report the results of our study of genetic differentiation between

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E. p. ozarkae from Missouri and E. p. phaeton from central New York.

#### Materials and Methods

Samples of *Euphydryas phaeton* were collected in the summer of 1982 from three areas in central New York and a single area in eastern Missouri. The New York collections were made near Slaterville Springs, Tompkins Co. (N=33); at the Oneonta Airport, Otsego Co. (N=30); and near Milford, Otsego Co. (N=26). The Missouri collection (N=28) was made at Merramec State Park, Franklin Co. The New York populations inhabited wet meadows; the Missouri population inhabited mesic woodland. All butterflies collected were stored in liquid nitrogen prior to electrophoretic analysis.

Allozyme variation was assayed at 25 presumptive gene loci, following the methods of May et. al. (1979). Details of electrophoretic methods and a table of electromorph frequencies are available from ATV on request. Electromorphic frequencies were calculated from direct counts of the electrophoretic phenotypes. Nei's (1972) measure of genetic similarity was used to quantify genetic differentiation between populations.

#### Results

There are very few differences in electromorph frequencies among the 3 New York and 1 Missouri populations of E. phaeton we examined. The average heterozygosity per locus is  $0.116 \pm 0.019$  (mean  $\pm$  S.E.) and the proportion of polymorphic loci is 0.80. Log-likelihood tests for heterogeneity in electromorph frequencies at each of the 25 loci (Sokal and Rohlf, 1981) illustrate the fundamental genetic similarity among the four populations. At only one locus (MPI) is there a heterogeneity significant at the p=0.05 level, and one expects to find such heterogeneity at the 0.05 level incorrectly in one in 20 such tests.

The genetic identities (Nei, 1972) further illustrate the similarities among the populations (Table 1). The three New York populations attributed to *E. p. phaeton* are somewhat more similar to each other (ave. I=0.989) than any of them is to the Missouri population attributed to *E. p. ozarkae* (ave. I=0.967), although all four populations are quite similar. The average genetic identity between *E. p. phaeton* and *E. p. ozarkae* that we report here is slightly less than that reported by Brussard et al. (1985), although their value (ave. I=0.991) was determined by electrophoresis of some of the same specimens. The discrepancy is due to a number of factors. We examined more specimens, especially of *E. p. phaeton*, but we used only 25 loci rather than the 28 they used. We felt on our further analysis that we could not score all loci with confidence. We also made some minor changes in scoring some of the loci we retained. All of these changes are minor, and none alters the conclusions made in the earlier work.

Table 1. Nei (1972) genetic identities and their standard errors (in parentheses) between three populations of *E. p. phaeton* from New York and one population of *E. p. ozarkae* from Missouri. Nei's index has a value of 1.0 for two populations that share all alleles at the same frequency, and a value of 0.0 for two populations that have no alleles in common. Abbreviations for the localities are as follows: MO = Merramec State Park, MO; NY1 = Slaterville Springs, NY; NY2 = Oneonta, NY; NY3 = Milford, NY.

	NY1	NY2	NY3
MO	0.977(0.018)	0.968(0.024)	0.956(0.033)
NY1		0.990(0.004)	0.989(0.006)
NY2			0.988(0.006)

#### Discussion

Lack of differentiation at allozyme loci does not preclude the possibility that the populations in question are reproductively isolated and therefore "good" species; in the absence of other evidence that isolation exists, however, it seems very unlikely that populations that are genetically so similar represent separate species. Sibling species in Lepidoptera for which data are available are clearly more different than these populations of E. phaeton. Angevine and Brussard (1979) analyzed differentiation at allozyme loci in populations of the satyrine butterflies Lethe eurydice and L. appalachia that fly in dissimilar but adjacent habitats within a few meters of each other. Although these Lethe species are morphologically nearly indistinguishable, the genetic similarity between them was I=0.865. Furthermore, although there were no diagnostic loci (i.e. one population fixed for an electromorph that does not occur in the other population), there were significant differences in electromorph frequencies at 5 of the 8 loci examined, and 4 of these were highly significant. Within the genus Euphydryas, sibling species are also genetically more distant from each other than are E. p. phaeton and E. p. ozarkae. The average genetic identity between E. editha and its two sibling species E. chalcedona and E. anicia is reported by Brussard et. al. (1985) to be I=0.837, and Euphydryas chalcedona and E. anicia, considered by those authors to be semispecies, have a genetic identity of I=0.858. (Here we are following the conservative nomenclature of Bauer (1975) rather than that of Miller and Brown (1981), since there are no justifiable reasons to separate North American Euphydryas into three separate genera (see Brussard et. al., 1985)). Non-sibling species of butterflies are even more distinct: within the genus Euphydryas average between-species identity is only I=0.674 (Brussard et. al., 1985); and among European pierids it is I=0.728 (Geiger, 1980).

Butterfly subspecies are on the average much more similar to each other than are sibling species. Table 2 shows genetic identities between subspecies in 3 genera of butterflies. All are high, most above I=0.950; and some (e.g., napi-bryoniae complex in Pieris) are probably not meaningfully different from unity. These subspecies, therefore, though recognizable on morphological or ecological grounds, and perhaps geographically distant from conspecific populations, are often genetically as similar as local populations. Brittnacher et. al. (1978) suggested that the availability of many visually discernible characters in Lepidoptera makes it easy to find morphological differences among local populations and to elevate some of these to races or subspecies. This may account for the low level of genetic differentiation detected among butterfly subspecies compared to that detected in *Drosophila*.

There are a number of visible phenetic or morphological differences between E. p. phaeton and E. p. ozarkae. The latter is larger and has reduced orange marginal markings on the ventral side of the wings. There are also the pronounced ecological differences in habitat and foodplant choice. Nonetheless, our analysis of allozymes reveals very little genetic difference among the populations we have examined, even though they are more than 1000 km apart. The lack of concordance between the ecological and morphological traits on the one hand and the electrophoretic traits on the other is not surprising. Singer (1982, 1983) has described variation in host plant preference among and within populations of E. editha, and has suggested how shifts in host plant use may evolve. Under strong selection, this evolution may occur relatively quickly. The comparatively slight allozyme differences, however, may have resulted from much weaker selection or none at all, and may indicate that the two lineages have been separate for only a short time. Such would be the case if, as a growing body of evidence now suggests (Wilson et. al., 1977; Thorpe, 1982), allozyme differences accumulate at a stochastically constant rate and thus may serve as a molecular evolutionary clock.

In summary, our results do not provide a definitive answer to the ques-

Table 2. Average genetic identities (Nei, 1972) between subspecies of butterflies.

Species	I	Reference
Pieris napi-bryoniae	0.992	Geiger, 1980
Speyeria callipe	0.983	Brittnacher et. al., 1978
S. coronis	0.929	Brittnacher et. al., 1978
S. zerene	0.982	Brittnacher et. al., 1978
Euphydryas editha	0.970	Brussard et. al., 1985
E. anicia	0.964	Brussard et. al., 1985
F. chalcedona	0.922	Brussard et. al., 1985
E. phaeton	0.967	This study

tion of the appropriate status of *E. p. phaeton* and *E. p. ozarkae*. Overall, there appears to have been little genetic differentiation between the two; however, the striking behavioral and ecological differences remain. Additional evidence from the field on the geographic distribution of the two types of populations and laboratory studies of degrees of interfertility would help to resolve this question.

Acknowledgments. Phil Koenig provided much useful information on E. p. ozarkae and assisted in collecting the specimens. Robert Lacy collected the New York samples. Deane Bowers and an anonymous reviewer offered many useful suggestions in the preparation of the manuscript. The electrophoresis was performed at Cornell University in the laboratory of Peter F. Brussard and supported by a grant, DEB 8116332, to him from the National Science Foundation. The administration of Merramec State Park, Missouri, permitted us to collect within the park; we thank them for their cooperation.

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# On the Monophyly of the Macrolepidoptera, Including a Reassessment of their Relationship to Cossoidea and Castnioidea, and a Reassignment of Mimallonidae to Pyraloidea

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There have been persistent reports that the closest relatives of various Macrolepidoptera are the Cossoidea or Castnioidea. Thus Brock (1971) claimed that butterflies evolved from Castnioidea, Bombycoidea (including Sphingoidea) evolved from Cossoidea, and Noctuoidea-Geometroidea evolved from Pyraloidea. Brock's paper is a worthwhile contribution to certain aspects of morphology of adult Lepidoptera, but he failed to place exact character changes on the branches of his tree, so his tree cannot be considered either phylogenetic in any sense, or phenetic, but rather intuitive (of course, every author claims that his tree represents the one and only true phylogeny, but other workers have the right to demand proof in terms of actual characters).

However, a detailed examination of Lepidopteran anatomy of all life stages reveals that a very large number of characters separate the Cossoidea and Castnioidea from the Macrolepidoptera, and that the Macrolepidoptera form a monophyletic group. The traits are listed below and numbered, and the numbers placed on the phylogenetic tree (Fig. 1) where they changed in the manner described in the text. For larval traits, see Fracker, 1915; Petersen, 1965; Forbes, 1923-1960, and Common and Edwards, 1981. For pupae, see Mosher, 1916; Common, 1974.

No doubt there are dissenting views, and the author has no great personal experience with moth anatomy; others should publish their phylogenies, provided that they are supported by actual character changes and their exact positions on the lineage, so that objective judgments may be made about them.

## Shared Derived Traits of Pyraloidea+Macrolepidoptera

(1) On the larva, the postnatal ("subprimary") seta L3 was lost on the prothorax, leaving only L1 and L2. Nearly all other moths have L1, L2, and L3. (2) On the larva, only one L seta is on abdomen segment 9 (other moths have several). This trait is variable in Pyraloidea, in which some Pyralidae subfamilies have two L setae on A9, and Pterophoridae have many secondary setae, but Thyrididae, Carposinidae, Alucitidae, Mimal-

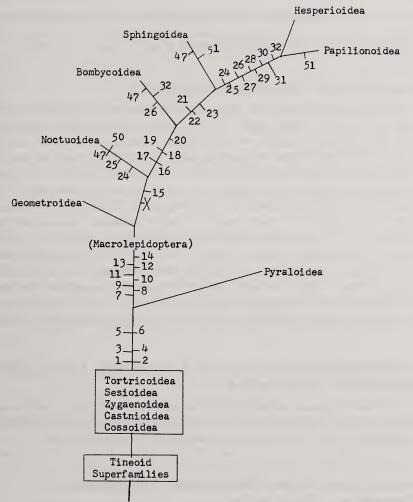


Fig. 1. Phylogeny of Ditrysian Lepidoptera. The numbers refer to gains, losses, or other alterations of the characters numbered and described in text (character 51 is in Table 1). X, possible origin of Bombycoidea-Sphingoidea, see text.

lonidae, and most Pyralidae subfamilies have only one L seta, indicating that one is the primitive state in the Pyraloidea. (3) On the pupal abdomen, only segments 5-6 (joints 4-5, 5-6, 6-7) are movable (in other Ditrysia, generally segments 3-7 move in males and 3-6 in females). (4) On the pupal abdomen, the segments lost their special spines and the pupa no longer protrudes from the larval burrow or cocoon (Tortricoidea, Sesioidea, Zygaenoidea, Castnioidea, and Cossoidea have two rows of backward-directed spines per abdomen segment used to wriggle out of the pupation site before adult emergence). The setose pupa of many Pterophoridae seems to be a later derivation; their long spines must have

another purpose entirely, as they lack a cocoon. (5) Wing vein M is vestigial in the discal cell (it is present, even branched, in most other moths). (6) Tympana evolved on the abdomen base.

#### **Shared Derived Traits of Macrolepidoptera**

(7) On the larval abdomen, setae L1 and L2 became far apart; they are close together in other moths. (8) On the pupa, maxillary palpi were lost. (9) The adult maxillary palpi shrank to minute size (they are 3-4 segmented in Pyraloidea and earlier moths). (10) The jugal fold was lost on the forewing base (Sharplin, 1964). (11) The CuP wing vein became rudimentary, rather than a distinct functional vein in earlier moths. (12) Inside the adult mesothorax, the discrimen (of Ehrlich, 1958) became large (it is small in other moths, though moderate in size in Cossoidea). (13) In the adult thorax, the third metatergopleural muscle assumed an advanced state (Sharplin, 1964). (14) The postmedian wing lever (median wing process of Sharplin, 1964) became large (it is usually small in other moths). In addition, all Macrolepidoptera have the heart looped to the top of the thorax, which may be another shared derived trait, though some microlepidoptera also have a looped heart (Hessel, 1969).

## Shared Derived Traits of Noctuoidea + Bombycoidea + Sphingoidea + Hesperioidea + Papilionoidea

(15) The tympana moved to the metathorax. The lack of additional shared derived traits allows for the possibility that the Geometroidea is polyphyletic, but I will leave this possibility to other workers.

### Shared Derived Traits of Bombycoidea + Sphingoidea + Hesperioidea + Papilionoidea

(16) Secondary larval setae became abundant on older larvae. (17) The larval crochets diversified into two or three lengths (only one length in most other moths). (18) The two adult ocelli were lost. (19) On the adult mesothorax wall, the upper sector of the paracoxal sulcus ("precoxal suture" of Brock) was lost (Brock's "precoxal suture" in skippers actually is the secondary sternopleural sulcus). (20) The tympanum was lost.

## Shared Derived Traits of Sphingoidea + Hesperioidea + Papilionoidea

(21) The cocoon was lost. (22) The adult antennae are distally enlarged (antennae vary in more primitive moths, but filamentous antennae occur in nearly all groups). (23) On the adult mesothorax wall, the parepisternal rift was lost (Brock, 1971).

#### Shared Derived Traits of Hesperioidea + Papilionoidea

(24) Eggs are upright. This is a rare condition, also possessed by Noctuoidea, and a few members within other moths (some Geometroidea, Choreutidae, Heliodinidae). Cossoidea and Castnioidea eggs have been stated to be upright, but actually both taxa have flat eggs (I. Common pers. comm.; Common and Edwards, 1981). (25) The larva has a ventral neck gland used for defense, as in Noctuoidea. (26) On the pupa, the foreleg femur is no longer visible as it is in nearly all moths. (27) The forewing lacks an areole, and vein R45 branches from R basad of R1 in the pupal wing (Zeuner, 1943). This areole occurs in most moths and in moths vein R<sub>45</sub> branches distad of R<sub>1</sub>. (28) On the adult mesothorax wall, the anapleural cleft is fused together and undetectable (Brock, 1971). (29) Inside the adult metathorax the furcal arms are mesally fused (Brock, 1971). (30) The adult heart is chambered where it loops to the top of the thorax (Hessel, 1969). The heart is looped in some moths, but only some Cossidae have a chambered heart (other Cossidae have only a ventral unchambered heart, indicating that the chamber of some Cossidae is just convergence). (31) On the adult abdomen, the anterodorsal apodemes on sternum 2 became minute (Brock, 1971). They are large in nearly all moths. (32) The adult wings lost the ability to be roofed over the abdomen.

I have not attempted to decipher the details of the phylogeny of the Ditrysians more primitive than Pyraloidea, except to determine that none of them are phylogenetically close to Macrolepidoptera. The most primitive Ditrysians, the Tineoid superfamilies, are distinguished from other Ditrysia by their (33) dual-rod coupling of abdomen sternum 2 with the thorax (Brock, 1971; Heppner, 1977). In addition, the Tineoid superfamilies (34) generally have only one row of backward-directed abdomen spines per segment (used to wriggle out of the cocoon or burrow), whereas Cossoidea, Castnioidea, Zygaenoidea, Sesioidea, and Tortricoidea have two rows per segment (see character 4). The latter five superfamilies are rather similar. The Sesioidea apparently branched from the Ditrysian trunk after the Cossoidea-Castnioidea-Zygaenoidea, after two wing base traits changed (Sharplin, 1964: (35) the metabasalare lost its connection to the episternum or prescutum; (36) the insertion of the third metatergopleural muscle changed to an advanced condition). Tortricoidea apparently appeared still later after the Ditrysian trunk evolved (37) a true pointed and crocheted cremaster (present in Tortricoidea, Pyraloidea, and Macrolepidoptera), setting the stage for the appearance of Pyraloidea.

The persistent suggestions that various Macrolepidoptera evolved independently from various primitive Ditrysia (Brock, 1971, argued that butterflies evolved from Castnioidea, and Bombycoidea from Cossoidea) seem wrong on both cladistic and phenetic grounds, as detailed below.

Butterflies show numerous differences from Castnioidea and Cossoidea

(see in particular Common, 1974), including the previous characters 1, 2, 3, 4, 5, 7, 8 (see Common and Edwards, 1981), 9, 10 (see Common and Edwards, 1981), 11, 12, 13, 16 (secondary setae absent or rare in Cossoidea-Castnioidea), 17, 18, 19, 21, 22 (antenna somewhat clubbed but plumosetipped in Castnioidea, simple to bipectinate in Cossoidea), 23, 24, 25, 27, 28, 29, 30, 31, 32, 35, 36, 37. In addition, the following traits differ between butterflies and Cossoidea-Castnioidea: (38) the larval crochets are in a circle or mesoseries in butterflies, in two transverse bands in Castnioidea and many Cossoidea; (39-40) the larval head is prognathous and strongly notched middorsally in Cossoidea-Castnioidea but not in butterflies; (41-43) the olfactory pits on the larval head are unusual in position in Cossoidea-Castnioidea (pit Pb is beside V1, La is far behind L1, Aa is near the P setae, Common and Edwards, 1981), normal in butterflies; (44) on the pupa, mandible remnants are definite bumps in Cossoidea-Castnioidea, but are weakly developed in butterflies (the "pilifers" of Mosher. 1916); (45) on the pupa a clypeolabral sulcus occurs in Cossoidea-Castnioidea but not in butterflies; (46) Cossoidea lack a proboscis, present in Castnioidea and butterflies; (47) chaetosema are absent in Cossoidea-Castnioidea, present in butterflies; (48) the mesepimeron on the adult thorax has a membranous division in most Cossoidea, lacking in Castnioidea and butterflies (Brock, 1971).

Obviously, these 41 traits demonstrate a vast gap separating Cossoidea-Castnioidea from butterflies. In fact, Cossoidea-Castnioidea are primitive members of the suborder Ditrysia, only slightly advanced from the Tineoidea. And the peculiar positions of the three olfactory pits (characters 41-43) on the larval head of Cossoidea-Castnioidea, (49) the lateral position of seta AF2 on the larval head (noted by Common and Edwards. 1981 and Hinton, 1946; my Zygaenidae larvae (first instar Zygaena trifolii) have these traits as well, except the position of pit Aa is normal), the absence of a proboscis, and the membranous epimeron cleft of Cossoidea surely indicate that the Cossoidea-Castnioidea-Zygaenoidea is a derived offshoot of the moth line which could not possibly have produced the butterflies or any other Macrolepidoptera. Evidently the superficial butterfly-like appearance, clubbed antennae, and day-flying habits of Castniidae have swayed the intuitive phylogenists, despite the vast morphological gap. Nevertheless, at least 16 families of moths have dayflying species with colorful wings, and the microscopic details of the antennae of Castniidae and Hesperiidae are very different (Jacqueline Miller, pers. comm.) despite their similar overall shape. Some Cossoidea have a chambered dorsal heart as in most butterflies (character 30), but other Cossids have the primitive ventral non-chambered heart (Hessel, 1969), so this must be convergence.

The story regarding the relationship between Sphingidae-Bombycoidea and Cossoidea-Castnioidea is much the same, though they are similar in these traits: the eggs of Bombycoidea are also flat (character 24), larvae

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lack the neck gland (25), a cocoon is present (21), chaetosema are absent (47), antennae are bipectinate in Bombycoidea as in some Cossoidea (22), the anapleural cleft is a rift (28), a parepisternal rift occurs in Bombycoidea (23), the metafurcal arms are more similar (29), and the sternal apodemes are longer (31). But there still remain some 34 traits separating Sphingoidea from Cossoidea-Castnioidea, and 32 separating Bombycoidea from them. Evidently certain superficial similarities between Bombycoidea and Cossoidea (bipectinate antennae, loss of proboscis, and the presence of secondary setae in Limacodidae (including Megalopyginae) and Bombycoidea, similar adult appearance of Megalopyginae and Lasiocampidae) led intuitive phylogenists to claim a relationship, but obviously the relationship is not genealogical.

The relationship between Cossoidea-Castnioidea and Geometroidea-Noctuoidea shows the same wide gap, of course. In addition, Noctuoidea have: (50) a unique MD2 seta present on T3 and A1 (present in Notodontinae and other Noctuidae, Hinton, 1946); and Geometroidea-Noctuoidea have tympana (characters 6, 15). It seems probable that their tympana are descended from that of Pyralidae, because the Geometroid tympanum is on the first abdomen segment as in Pyralidae, and the Noctuoid tympanum, which moved to the metathorax, retains a hood on the first abdomen segment and commonly has a ventral abdominal pouch that may have once possessed a tympanum. The Noctuoid tympanum shows sufficient variation as to allow for the possiblility that it is descended from the abdominal type.

The internal phylogeny of Macrolepidoptera seems straightforward except for the placement of Bombycoidea and Sphingoidea (see Table 1). The Geometroidea and Noctuoidea seem the most primitive Macrolepidoptera because their larvae generally lack secondary setae and retain one-length (uniordinal) crochets, their pupae retain the temporal cleavage line and the visible prothorax femur, their adults retain ocelli, tympana, and the upper sector of the paracoxal sulcus, and with Bombycoidea their adults retain the parepisternal rift and an areole. The Geometroidea with its flat eggs, abdominal tympana (as in Pyraloidea), and merely pectinate (not bipectinate) antenna is the more primitive of the two.

The most advanced group of Macrolepidoptera, butterflies, shares several derived traits with Noctuoidea: upright eggs, and a ventral larval neck gland used for chemical defense. While the latter gland may be convergent, or lost in other Macrolepidoptera, the upright eggs of butterflies-Noctuoidea are nearly unique (except in Heliodinidae, Choreutidae, and some Geometridae; the Cossidae, including Cossinae, and Castniidae always have flat eggs, I. Common, pers. comm. and Common and Edwards, 1981). If the upright egg is genuinely co-ancestral then the Bombycoidea-Sphingoidea branched off at point X of Figure 1. However, using the characters and weights of Table 1, the tree of Figure 1 is the most

Table 1. Characters of the Macrolepidoptera superfamilies. F, flat; U, upright; +, present; -, absent; M, mesoseries (medial crescent); O, oval; B, biordinal (two lengths); U, uniordinal; T, triordinal; S, simple or filamentous; P, pectinate (two projections from each antenna segment); B, bipectinate (four projections); C, clubbed. In addition, traits 28-31 are derived traits of butterflies (Hesperioidea-Papilionoidea), and 50 is a derived trait of Noctuoidea.

	Geometroidea	Noctuoidea	Bombycoidea	Sphingoidea	Hesperioidea	Papilionoidea	ght
Trait	Geor	Noct	30m	Sphi	Iesp	Papi	Weight
16 secondary	· ·	F	-	92	-		
setae	<u>.</u>		++	++	++	++	1
17 chrochet	(+ prolegs)	(+ rarely)					
length	B(U)	U(B)	В	В	T(B)	T(B)	1/2
18 ocelli	±.	±.	-		- (2)	-	1/2
19 upper sector	_						
of paracoxal							
sulcus	±	土	-	-	-	-	1/2
20 tympana	土	土	-	-	-	-	1/2
21 cocoon	+	+	+	-	-	-	1
22 antenna			(-)				
shape	S,P	B,P,C,S	B,P	С	С	С	1/2
•	,	, , ,	,	(P rare, short)			
23 parepisternal				·			
rift	±	土	土	-	-	-	1/2
24 egg	F	U	F	F	U	U	1
25 ventral neck							1
gland on larva 26 foreleg femur	- on	±	-	-	土	土	1
pupa visible	on <u>+</u>	±	-	±		-	1/2
27 areole	±	±	土	_ ±	-	-	1
32 wings roofed o							
abdomen	土	±	-	土	-	-	1/2
38 crochet							
arrangement	M	M	M	M	0	M old O young	1/2
47 chaetosema	±	-	-	-	+	+	1/2
51 temporal cleav	vage						
line of pupa	±	±	±	-	+	-	1

parsimonious, requiring the fewest character changes of any of the possible trees. This is partly because the Bombycoidea-Sphingoidea-butterfiles share certain traits (crochets always bi- or triordinal, secondary setae abundant, tympana and ocelli lost, and the upper sector of the paracoxal sulcus lost. Because three of these traits represent losses, there is some doubt about this parsimonious scheme, and first-instar butterflies have primary setae, whereas first-instar Bombycoidea-Sphingoidea apparently do not. Hopefully current and future research will add more characters to the table to resolve this question. At the present time Figure 1 seems most probable, which suggests that the ancestor of Bombycoidea-Sphingoidea-butterflies was a dayflier, resulting in the loss of tympana and ocelli, and the development of colorful wings. Sphingoidea and butterflies do share the loss of a cocoon and a roughly similar antenna.

Eye morphology may provide relevant characters within Macrolepidoptera (Horridge, 1975), and demonstrates similarities between skippers and other Macrolepidoptera. Many large nocturnal moths and skippers have a clear zone in the eye, and skippers are similar to Bombycoidea in having retinula cell extensions across the clear zone to the lens system (but skippers differ from Bombycoidea and others in lacking any anatomical wave guides) and skippers resemble Agaristidae in lacking pigment in the clear zone in daylight. Skippers and some night-adapted Macrolepidoptera have a well-focused eye, unlike Papilionoidea (one spot on the retina receives light focused from many ommatidia besides its own).

It should be noted that Mimallonidae (=Lacosomidae=Perophoridae), which have secondary setae only on the prolegs (Forbes, 1923, gives a setal map), have been placed in Bombycoidea and Geometroidea, but various traits place them in the Pyraloidea: abdominal setae L1 and L2 adjacent; sometimes two (or one) L setae on abdominal segment 9 (Fred Stehr, pers. comm.); only two postnatal prothorax L setae; crochets in a circle; a well-developed CuP vein.

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## Electrophoretic Confirmation of the Species Status of Pontia protodice and P. occidentalis (Pieridae)

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Abstract. Electrophoretic study of sympatric and allopatric populations of the taxa *Pontia protodice* and *P. occidentalis* demonstrates unequivocally that they represent closely related but independent gene pools. Each is genetically very homogeneous over its geographic range, strongly suggesting high levels of migration, colonization, and/or gene flow. *P. protodice* is less like European *P. callidice* than is Californian *occidentalis*, suggesting a possible phylogeny which agrees with previous inferences from morphology and biogeography.

#### Introduction

The taxa Pontia (or Pieris or Synchloe) protodice Bdv. & LeC. and P. occidentalis Reak. have posed an ongoing problem for Lepidopterists; though Chang (1963) demonstrated morphological differences between them and Shapiro (1976) summarized the by then copious biological and distributional information on hand—all of which tended to support their status as separate species—many workers, including some professionals, have remained unconvinced and profess to be unable to classify many specimens to one species or the other. The present study was undertaken in the hope of further clarifying their status by comparing population samples of both from areas of sympatry and allopatry, using electrophoresis to quantify genomic similarities and differences. An ancillary objective was to test the prediction that both species would show very little interpopulational differentiation, due to their apparent pattern of colonization and their epigamic behavior.

#### Materials and Methods

The sources of our samples are listed in Table 1. All animals were transported alive and immediately stored at -70°C until electrophoresis. Only 1984 and 1985 catches were used. All animals were determined as protodice or occidentalis by AMS, using wing phenotype, and all wings were saved for post-electrophoresis verification. Only one possibly ambiguous specimen was used in the study. The head and thorax of each



Fig. 1. Localities for California samples. Abbreviations, numbers and makeup by species as in Table 1.

butterfly were homogenized in 4 volumes of Tris-HCl buffer (0.05 M, pH 8.0). We used horizontal starch gel electrophoresis, following slightly modified standard procedures (Ayala et al., 1972; Geiger, 1981). Twenty-three enzymes were scored: acid phosphatase (locus ACPH), adenylate kinase (AK-1, AK-2), aldolase (ALD), arginine kinase (APK), fumarase (FUM), glutamate-oxaloacetate transaminase (GOT-1, GOT-2), glutamate-pyruvate transaminase (GPT), glyceraldehyde-phosphate dehydrogenase (GAPDH),  $\alpha$ -glycerophasphate dehydrogenase ( $\alpha$ -GPDH), hexokinase (HK), indophenol oxidase (IPO), isocitrate dehydrogenase (IDH-1, IDH-2), malate dehydrogenase (MDH-1, MDH-2), malic enzyme (ME-1, ME-2), phosphoglucomutase (PGM), 6-phospho-gluconate dehydrogenase (6-PGD), phosphoglucose isomerase (PGI), and pyruvate kinase (PK).

Analysis of the progeny of parents with different phenotypes in *Pieris brassicae* L. (Geiger, 1982) was the basis for interpreting zymograms of polymorphic loci. No deviation from the pattern observed in *P. brassicae* has been found in any individual investigated in this study. The distributions of alleles are also in good accord with Hardy-Weinberg expectations.

The most frequent allele ("common allele") in *P. brassicae* was used as a standard. This allele is designated with the index 100. Electromorphs with different mobilities are designated in relation to this standard; an allele

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Table 1. Localities for samples used in this study, with notes on sympatry.

California: Lassen County: 2.5 km S Adin, 1500 m, 11.viii.1985 (n=24)(AD), occidentalis abundant, protodice unrecorded but possible infrequent immigrant. Siskiyou County: Ball Mountain, 2175 m, 10.viii.1985 (n=28)(BM), occidentalis only, very abundant. Sierra County: Sierra Valley, 4 km NE Sierraville, 1500 m, 25-30.vii.1985 (n<sub>prot.</sub> =55, n<sub>occ.</sub> =46)(SV), both abundant and permanently sympatric. Placer and Nevada Counties: Donner Pass, 2100 m, 15.viii.1985 (n<sub>prot</sub> = 6, n<sub>occ</sub> = 4)(DP), occidentalis common resident, protodice frequent immigrant, overwintering once in 14 yr. Nevada County: Castle Peak, 2750 m, 6.vii.1985 (n=26)(CP), occidentalis only (14 yrs. of observation). Alpine County: Leviathan Peak, 2800 m, 25.vii.1984 (n<sub>prot.</sub> = 2, n<sub>occ.</sub> = 17) (LP), occidentalis common resident, protodice immigrant. Mono County: nr. Mono Lake, 1800 m, 2.vii.1985 ( $n_{prot.} = 17$ ,  $n_{occ.} = 2$ )(ML), protodice common, occidentalis infrequent (but commoner at higher elevations). Kern County: Lake Isabella, 780 m, 16.viii.1985 (n=19) (LI), protodice only. San Bernardino County: Route 38 N Onyx Summit, elevations not available, 15.vi.1985 (n=3)(OS), protodice only.

**Nevada:** Churchill County: vic. Fallon, 1250 m, 13.viii.1984 (n=30), protodice abundant, occidentalis very rare (none taken).

**Florida:** Broward County: vic. Davie, metropolitan Miami, 25.iv.1984 (n=9), protodice only.

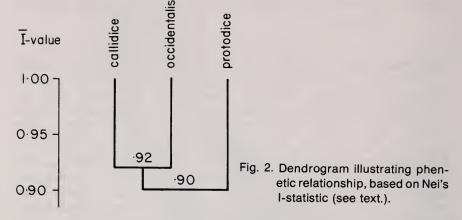
**Mexico:** Distrito Federal: Xochimilco-San Gregorio, 27.vi-2.vii.1984 (n=12), protodice only.

105, then, codes for an enzyme that migrates 5 mm faster than the P. brassicae variant.

The statistic  $\overline{\mathbf{I}}$  (Nei, 1972) was used to estimate the genetic similarity between the samples over all loci. The calculated  $\overline{\mathbf{I}}$ -values for the pooled samples of the two North American taxa plus P. callidice Hübner have been used to construct a dendrogram (Fig. 2) by cluster analysis (UPGMA method, Ferguson, 1980). The  $\overline{\mathbf{I}}$ -values for the pooled samples are based on only 22 loci (without ACPH) to make the data comparable to an earlier study (Geiger and Scholl, 1985).

#### Results

At 16 of the 23 loci compared, protodice and occidentalis show only very low polymorphism (f\_common allele  $\geq$  0.98), and share the same common allele (ALD, AK-1, AK-2, APK, FUM, GADPH, GOT-2, &-GPDH, IDH-1, IDH-2, IPO, MDH-2, ME-1, ME-2, 6-PGD, PK). At four other loci (GOT-



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1, MDH-1, PGM, PGI) the two taxa have the same common allele in all samples, but are polymorphic (Table 2). For those samples with  $n \ge 10$ , the frequencies of all alleles are remarkably similar and show no statistically significant interpopulational differences. The situation is different for the three remaining loci (ACPH, HK, GPT) (Table 3). There are two alleles at the GPT locus which are found in both taxa but at very different frequencies: the common allele in protodice (GPT 86) is found at very high frequency ( $f \ge 0.96$ ) in all samples of that taxon but at much lower frequencies ( $f \le 0.25$ ) in the occidentalis samples. The allele 97 is the common GPT allele in occidentalis ( $f \ge 0.75$ ) and is very rarely recorded in protodice ( $f \le 0.04$ ). The genetic differences between the taxa are even more pronounced at the HK locus, where only the allele 93 is found in protodice (f = 1.00); this allele occurs in occidentalis only at frequencies  $\le 0.02$ . At the ACPH locus each taxon is monomorphic for a different allele.

It is important to underscore the fact that there were no heterozygous individuals for the ACPH locus at those localities where the taxa are frequently to permanently sympatric (Donner, Sierra Valley—see Table 1). The one possibly ambiguous individual, a female from Sierra Valley, was electrophoretically "pure protodice," which taxon it most closely resembled in wing phenotype. The frequencies of heterozygotes for HK and GPT did not vary significantly between sympatric and allopatric samples.

The very similar allelic frequencies at all loci among population samples result in very high  $\overline{\mathbf{I}}$ -values for the within-taxon comparisons ( $\overline{\mathbf{I}}_{occidentalis} = 1.00$ ,  $\overline{\mathbf{I}}_{protodice} \geq 0.99$ ) (Table 4). When the two taxa are compared the  $\overline{\mathbf{I}}$ -value is (as expected) lower,  $\mathbf{x}_{(I)} = 0.88 \pm 0.01$ .

Because HJG had already studied European *P. callidice*, and there has been considerable speculation concerning its relationship to the American taxa (Higgins and Riley, 1970; Shapiro, 1980), we compared it to our results using the 22 loci (omitting ACPH) studied for all three taxa.

Table 2. Allelic frequencies at polymorphic loci.

		n animals	GOT-	_	120	125	MDH-	_	PGM 90	95	103	107	109	PGI 87	97	107	115	125
	Sierra Valley	55		.18	.81	.02	.97	.03		.07	.90	.03		.02	.06	.84	.08	
	Lake Isabella	19		.05	.95		.84	.16	.03	.10	.84	.03		.03	.05	.89	.03	
	Mono Lake	17		.12	.85	.03	.88	.12	.03	.12	.85				.06	.91	.03	
	Donner Pass	6		.17	.67	.17	.92	.08		.08	.75	.17			.25	.75		
e	Fallon	30		.17	.82	.02	1.0		.02	.08	.80	.10			.03	.92	.05	
protodice	Florida	9		.28	.72		.95	.05			1.0					1.0		
pro	Mexico	12		.13	.87		.96	.04	.04	.04	.88		.04		.08	.88		.04
	all samples	153		.15	.83	.02	.95	.05	.01	.08	.86	.04	.01	.01	.06	.88	.04	.01
	Ball Mtn	28		.07	.79	.14	1.0			.07	.75	.16	.02		.04	.93	.04	
s	Adin	24	.02	.10	.71	.17	1.0			.08	.75	.15	.02		.06	.85	.08	
tali	Sierra Valley	46		.07	.79	.14	.97	.03	.01	.03	.76	.20		.01	.03	.90	.05	
occidentalis	Castle Peak	26		.02	.81	.17	.90	.10		.02	.71	.23	.04		.04	.89	.08	
	Leviathan	17		.03	.74	.23	1.0			.09	.74	.18			.12	.82	.06	
	all samples	147	.01	.06	.77	.17	.97	.03	.01	.05	.75	.18	.01	.01	.05	.88	.06	

Table 3. Allelic frequencies at loci with high variability between the taxa.

		n animals	АСРН 88 95	GPT 86 97	нк 93 96
	Sierra Valley	55	1.0	.99 .01	1.0
	Lake Isabella	19	1.0	1.0	1.0
	Mono Lake	17	1.0	.97 .03	1.0
	Donner Pass	6	1.0	1.0	1.0
ice	Fallon	30	1.0	1.0	1.0
protodice	Florida	9	1.0	1.0	1.0
pro	Mexic <sub>O</sub>	12	1.0	.96 .04	1.0
	all samples	153	1.0	.99 .01	1.0
	Ball Mtn	28	1.0	.23 .77	.02 .98
S	Adin	24	1.0	.23 .77	.02 .98
ıtali	Sierra Valley	46	1.0	.13 .87	.02 .98
occidentalis	Castle Peak	26	1.0	.25 .75	1.0
000	Leviathan	17	1.0	.06 .94	1.0
	all samples	147	1.0	.18 .82	.01 .99

Occidentalis and callidice cluster at a slightly higher level than protodice. The relationships with other species of the genus Pontia remain unchanged.

#### Discussion

We had predicted a high level of genetic similarity over large distances in these species because both are highly vagile, colonizing or "weedy" species and because P. occidentalis is a facultative "hilltopper," a mating strategy which would tend to promote gene flow and prevent local ecotypic differentiation. (For discussion of the population dynamics of P. protodice, see Shapiro, 1979; for dispersal ability of P. protodice, Shapiro, 1982 and of P. occidentalis, Shapiro, 1977; an explicit prediction was made in Shapiro, 1984, p. 181). We were nonetheless surprised at the extreme homogeneity of protodice over a continent-wide range (Florida, Mexico, Nevada, California). We know that these populations are not so homogeneous for such adaptive traits as the photoperiodic thresholds for induction of pupal diapause, the programming and control of diapause, hostplant adaptation and disease resistance (AMS, unpublished data). Mexican protodice also lay smaller eggs than other populations, even under standardized rearing conditions and on a standard diet (Shapiro, in press). All protodice populations tested to date have been fully reproductively compatible with one another, even in such wide crosses as New York

Table 4. I-values for the comparison of all populations samples (n > 6) based on the data of 23 enzyme loci.

protodice							occidentalis				
-	Lake Isabella	Mono Lake	Donner Pass	Fallon	Florida	Mexico	Ball Mtn	Adin	Sierra Valley	Castle Peak	Leviathan
Sierra Valley	1.00	1.00	1.00	1.00	1.00	1.00	.89	.89	.88	.89	.87
Lake Isabella		1.00	1.00	1.00	1.00	1.00	.89	.88	.88	.89	.87
Mono Lake			1.00	1.00	1.00	1.00	.89	.89	.88	.89	.87
Donner Pass				1.00	.99	1.00	.88	.89	.88	.88	.87
Fallon					1.00	1.00	.89	.89	.88	.89	.87
Florida						1.00	.89	.89	.88	.88	.87
Mexico							.89	.89	.88	.89	.87
Ball Mtn								1.00	1.00	1.00	1.00
Adin									1.00	1.00	1.00
Sierra Valle <b>y</b>										1.00	1.00
Castle Peak											1.00

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X California or Texas, or Mexico X California; but the control of diapause is routinely disrupted in such wide crosses, usually resulting in failure to diapause or very rapid spontaneous termination, and much less often in extended, lethal diapause. We have less extensive experience crossing occidentalis populations but have found complete compatibility among California and Colorado ones and between California and the Alaskan subspecies nelsoni Edwards (Shapiro, 1975) which is highly incompatible with European callidice (Shapiro, 1980). Diapause is largely unstudied in these cases.

Vawter and Brussard (1984) found similar uniformity in the weedy, introduced species *Pieris rapae* L. in eastern North America, but more genetic diversity in the west. Populations of *P. rapae* in the west are discontinuous, separated (except in the Central Valley of California) by broad expanses of inhospitable terrain. The ability of *P. rapae*, as an obligatorily multivoltine species, to accommodate to western climates by altitudinal migration seems very limited in comparison to *P. protodice*; indeed, *rapae* is largely confined to local "mesic" pockets created by irrigation within arid or semiarid regions, while *protodice* is able to colonize throughout. This is most dramatically illustrated in central Mexico: *protodice*, a native species, is quite generally distributed, but the introduced *rapae* is ecologically "trapped" in the floating gardens of Xochimilco, near Mexico City, where continuous breeding is possible. It is hardly surprising that the homogenizing effects of gene flow are more evident in *P. protodice* than in *P. rapae*.

Vawter and Brussard argue that gene flow should be countered in colonizing or fugitive species by genetic drift and founder effect, which would tend to cause stochastic differences among populations. We are examining the genetic structure of truly ephemeral populations of  $P.\ protodice$  (presumably resulting from colonizations by single females) in the hope of addressing this question.

The clear genetic differences between protodice and occidentalis at three loci are in sharp contrast to the low variation within the taxa. The most important samples are those from Sierra Valley, where both taxa are very abundant and apparently in stable coexistence (over 10 years, AMS observations) and where occasional (<3%) ambiguous phenotypes are encountered. There is absolutely no evidence for gene flow in the sympatric Sierra Valley samples; the lack of ACPH heterozygotes shows that there were no  $F_1$  hybrids in our collections. There may indeed be occasional, very rare spontaneous hybridization (AMS has collected one mixed pair in copula in Donner Pass), but the electrophoretic data provide clear confirmation that protodice and occidentalis represent separate gene pools, corresponding to biological species. There is no evidence of introgression (that is, the two taxa are not more similar genetically in sympatry than in allopatry).

It is exceedingly difficult to hybridize these two taxa spontaneously, and

pairings can normally only be secured with a pre-excited male and a substituted *teneral* allospecific female. Hand-pairings are easily achieved, but to date the level of developmental incompatibility has been high, resulting in dwarfing, high mortality, malformation, deficiency of the heterogametic sex (female), and hybrid sterility. Further information on experimental hybridization will be published elsewhere; it suffices to note that it is fully in accord with the electrophoretic results.

Genetic differences within the group of three taxa (protodice, occidentalis, callidice) are relatively low but within the range previously reported for closely-related species in Pieridae (Geiger, 1981; Geiger and Scholl, 1985). This observation can be interpreted as evidence for the recency of speciation in that group. Shapiro (1980) interpreted the group as derived by fragmentation of the range of a widespread circumglacial steppetundra entity more or less resembling the climatic adaptation of some contemporary occidentalis populations. The phenotypic characteristics of protodice are clearly derivative reductions from the full occidentalis pattern, which in the western United States is polyphenic and shows some reduction from the *nelsoni-callidice* pattern. Larval and pupal characters vary concordantly (Shapiro, unpublished data). The dendrogram thus further supports the proposed phylogeny, which would derive occidentalis from circumpolar proto-callidice and protodice in turn from occidentalis, without specifying time scales. Certain central Asian taxa assigned as subspecies to callidice (orientalis Alph., kalora Moore, etc.) are extremely close phenotypically to western North American occidentalis. This may represent parallel evolution in similar climates—but then again, it may not. Nominate callidice from the Alps and Pyrenees seems to represent the extreme end of a long cline, physiologically as well as geographically.

We note in closing that the extreme genetic homogeneity shown by *protodice* and *occidentalis* over a large range suggests the reality of a "general purpose genotype" associated with weediness and physiological adaptability (Baker, 1965) and the utility of these common animals as vehicles to get a closer look at its structure.

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# Susceptibility of Eggs and First-Instar Larvae of Callosamia promethea and Antheraea polyphemus to Malathion<sup>1</sup>

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**Abstract.** Susceptibility levels to malathion water emulsions are established for *Callosamia promethea* (Drury) and *Antheraea polyphemus* (Cramer): *C. promethea* eggs,  $LC_{50} = 0.1$  mg/ml, probit = 3.3 + 0.9 (log conc); *C. promethea* 1st-instar larvae,  $LC_{50} = 0.01$  mg/ml, probit = 11.3 + 2.9 (log conc); *A. polyphemus* eggs,  $LC_{50}$  between 15.6 and 31.2 mg/ml; *A. polyphemus* 1st-instar larvae,  $LC_{50} = 0.06$  mg/ml; probit = 9.9 + 4.1 (log conc); *C. promethea* embryos,  $LC_{50} = 248$  mg/ml, probit = -2.3 + 3.0 (log conc).

#### Introduction

Giant silkworm moths, such as Callosamia promethea (Drury) and Antheraea polyphemus (Cramer), used for research purposes, are reared on foliage obtained in agricultural or domestic situations where organophosphate insecticides may be applied or stored. Information is not available on the susceptibility of the early stages of these giant silkworm moths to foliar applications or organophosophate insecticides. To estimate the susceptibility of these insects to natural, potentially contaminated foliage, we determined the laboratory susceptibility of eggs and 1st-instar larvae of C. promethea and A. polyphemus to malathion, 0,0-dimethyl phosphorodithioate of diethyl mercaptosuccinate, a representative, commonly-used organosphophate material. These estimates of susceptibility are based on laboratory testing procedures, and do not account for field conditions (e.g., pH, temperature, humidity, residue age) that might alter the effective toxicity of the malathion.

#### **Materials and Methods**

Test insects were obtained from colonies of C. promethea and A. polyphemus reared in sleeve cages on wild cherry (Prunus serotina) or

<sup>&</sup>lt;sup>1</sup>Lepidoptera: Saturniidae. This research was not supported by public funds. The opinions contained herein are those of the authors and should not be construed as official or reflecting the views of the Department of the Army.

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various maples (Acer spp.) for 10-12 generations. Ortho Malathion 50 Insect Spray<sup>R</sup> (Chevron Chemical Company Ortho Division, San Francisco, CA 94119, EPA Reg. No. 239-739-AC) an emulsifiable concentrate containing 50 percent actual malathion by weight (521 mg/ml), was used for all testing. The appropriate quantity of emulsifiable concentrate was added to water with a volumetric pipet to make a stock emulsion. The stock emulsion was diluted with water, with constant stirring of stock and dilutions, to produce the test concentrations. For larvicide tests, individual hostplant leaves were dipped in test emulsions for 30 seconds and allowed to air dry. Control leaves were dried separately after being dipped only in water. Unfed, 1st-instar larvae (<24 hours old) were placed in random sequence on the treated and control leaves and held in plastic cups and covered with facial tissues for 48 hours before recording mortality. For ovicide tests, egg masses (<48 hours old) were dipped in random sequence in test emulsions for 30 seconds, then allowed to air dry. Control egg masses were dipped in water only, then allowed to air dry separately. Mortality of treated eggs was determined as those that failed to hatch after all control eggs hatched. Embryos of C. promethea were tested at high concentrations of malathion (up to 500 mg/ml) to determine the existence of a concentration-mortality relationship. The percentage of embryo mortality rather than the hatch failure was the measured criterion. Mortality data on embryos, eggs, and larvae were subjected to probit analysis using a computer program package described by Barr, et al. (1976).

#### Results and Discussion

The label recommended concentration for spray application of malathion water emulsion to fruit and ornamental foliage is 12.0 mg AI/ml. Table 1 shows that both eggs and 1st-instar larvae of C. promethea and 1st-instar larvae of A. polyphemus were highly susceptible to recommended doses. The concentration-mortality relationships for C. promethea eggs and 1st-instar larvae are shown in Figures 1 and 2. Eggs of A. polyphemus were not susceptible at label concentrations; those exposed to concentrations of up to 15.6 mg/ml showed no ovicidal effects, while those exposed to concentrations of 31.2 mg/ml and above showed no hatch. No concentration-mortality relationship was established for A. polyphemus eggs. The concentration-mortality relationship applicable to A. polyphemus 1st-instar larvae is shown in Figure 3. Embryos of C. promethea were not susceptible to label concentration of malathion water emulsion (Table 1). However, toxicity to embryos was observed at the higher concentrations used in initial range finding. In some of these tests, fullyformed larvae were present in the eggs, but did not hatch. In C. promethea the developing dark larva imparts a gray hue to the otherwise white egg. The presence of larvae in the "gray" eggs was confirmed by dissection.

Table 1. Malathion susceptibility of eggs and larvae of *Callosamia promethea* and *Antheraea polyphemus*.<sup>1</sup>

Stage Tested	Number Tested	$\mathrm{LC}_{50}$	$\mathrm{LC}_{90}$	Relative Susceptibility $^2$ at $\mathrm{LC}_{50}$
		Callosan	nia promethe	ea
Embryos	450	248	659	0.05
Eggs	650	0.1	0.36	120
1st-Instar				
Larvae	380	0.01	0.02	1200
		An the rae	ea polyphem	us
Eggs <sup>3</sup>	120	>15.6	>15.6	>0.77
1st-Instar				
Larvae	280	0.06	0.13	200

<sup>1</sup>all values in mg/ml

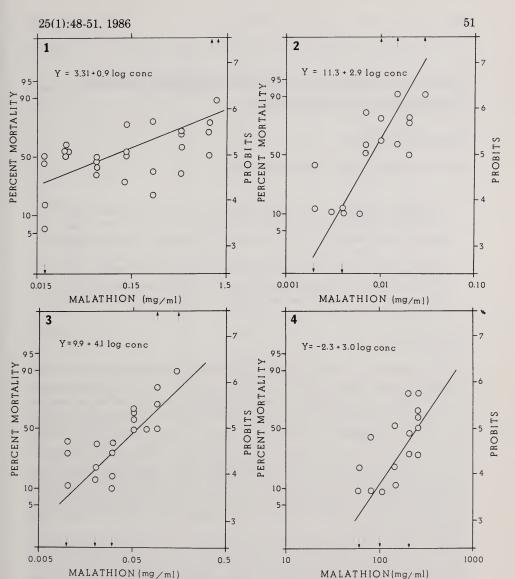
<sup>2</sup>label concentration/lethal concentration (LC<sub>50</sub>)

<sup>3</sup>no ovicidal effects observed at 15.6 mg/ml

This condition was not observed in ovicide tests with A. polyphemus because the light yellow larvae are not visible through the tan egg shells and no dissections were performed. Tests conducted with high concentrations of malathion (Figure 4) demonstrated that a concentration-mortality relationship existed.

Mortality preceding eclosion of eggs has been observed in many lepidopterans in connection with exposure to ovicides, but the phenomenon in general is poorly understood (Smith & Salkeld, 1966). Potter, et al. (1957) reported that high concentrations of TEPP (tetraethyl pyrophosphate) caused mortality in eggs of *Pieris brassicae* Linnaeus; older eggs being considerably more susceptible than younger ones. They concluded that toxicity due to organophosphate exposure appears to involve cholinesterase inhibition at some stage of embryonic development. The *C. promethea* eggs we tested were less than 48 hours old. For those exposed to malathion water emulsion at 0.01 mg/ml all of the embryos developed, but only 50 percent hatched; for those exposed to 248 mg/ml only 50 percent of the embryos developed and none hatched.

These studies establish baseline susceptibility of immature stages of *C. promethea* and *A. polyphemus* to malathion water emulsions, and demonstrate that the immature stages are susceptible at recommended dosages. The particular hazard presented by malathion, or other more toxic or more persistent organosphosphate materials, depends on other variables, such as pH, temperature, humidity, and residue age, not included in these studies.



Figs. 1-4. Susceptibility of Giant Silkworm Moth Eggs and Larvae to Malathion Water Emulsion: 1. Callosamia promethea Eggs; 2. Callosamia promethea 1st-Instar Larvae; 3. Antheraea polyphemus 1st-Instar Larvae; 4. Callosamia promethea embryos.

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# Pupal Mortality in the Bay Checkerspot Butterfly (Lepidoptera: Nymphalidae)

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Abstract. Mortality for pupae of *Euphydryas editha bayensis* (Lepidoptera: Nymphalidae) placed in the field ranged from 53 to 89%. Predation and cold weather during the period of pupation were the major mortality factors. Mortality during this stage is high enough to affect total numbers of adults and other life stages and variable enough to affect the population dynamics of these butterflies. Studies of these and other holometabolous insect species should include estimates of pupal mortality.

#### Introduction

Few complete life tables have been published for natural populations of butterflies (see Dempster, 1983). This is partly because at least one life stage of these holometabolous insects is difficult or impossible to observe in the field. For example, *Euphydryas editha bayensis* Sternitzky (1937) (the Bay Checkerspot butterfly) is among the most thoroughly studied insects, but only its adult stage is easily observable. Eggs and prediapause larvae have only recently been found in numbers, and diapausing larvae remain essentially a "black box" to us. Many post-diapause larval samples have been collected and some data on parasitoid rates have been published (Ehrlich, 1965; White, 1973 and Stamp, 1984). Pupae are almost never seen.

Prior to this study the only information on pupal mortality in *Euphydryas editha* was Singer's observation that several out of 20 pupae placed out at Jasper Ridge were eaten and the wooden tongue depressors used to mark them had been chewed on by rodents (Singer, 1971).

Life table data for butterfly populations that have been published show pupal mortalities ranging from 0 to 100%, but averaging around 60% (Table 1). Most of the pupal mortality identified was due to predation. With this background I did an experiment designed to quantify pupal mortality in the Bay Checkerspot butterfly.

#### Materials and Methods

Large post-diapause larvae were collected in late February and early March from field sites at Edgewood Park (EW) in 1982 and 1983 and Morgan Hill (MH) in 1984. Both sites are serpentine grasslands (Krucke-

Table 1. Available data on lepidopteran pupal mortality.

Species	Pupal Mortality	Major Factor	n	Source
Pieris rapae	.31	parasitoids	large	Harcourt 1966
•	.38	virus	42	Dempster 1967
	.08	virus	27	Dempster 1967
	.05	virus	65	Dempster 1967
Papilio machaon	.59	predation	150	Wiklund 1975
<u>r</u>	.90	predation	158	Wiklund 1975
Papilio xuthus	.83	parasitoids	12	Watanabe 1976
*	.12	predation	25	Watanabe 1976
Artopoetes pryeri	.45	predation	42	Watanabe & Omata 1978
Papilio glaucus	1.00	predation	112	West & Hazel 1982
. 0	.80	predation	109	
	.88	predation	128	
	.55	predation	127	
Battus philenor	.91	predation	140	West & Hazel 1982
	.94	predation	139	
	.77	predation	80	
	.96	predation	80	
Battus philenor	.14	predation	64	Sims & Shapiro 1983
	.67	predation	109	
Agraulis vanillae	.08	predation	364	I.L. Brown pers. comm.

berg, 1984; Sommers, 1984; Crittenden and Grundmann, 1984) where adverse soil conditions favor the native plants on which the butterflies depend. Edgewood Park is in San Mateo County at 37° 27′ 50″ latitude, 122° 17′ 10″ longitude, and 660′ (200m) elevation. Morgan Hill is in Santa Clara County at 37° 11′ 28″ latitude, 121° 40′ longitude, and 1000′ (300m) elevation. For comparison, Jasper Ridge is in San Mateo County at 37° 25′ latitude, 122° 19′ longitude, and 550′ (170m) elevation. Rainy weather in 1982 and 1983 and a large population in 1984 (at MH) allowed longer collection periods than normal. Larvae were kept in groups of about four in plastic petri dishes (37mm in height, 150mm diameter) and fed daily until they pupated, on average about a week. They were fed primarily the Eurasian weed *Plantago lanceolata* L., which they seem to prefer in the laboratory but which is rarely used in the field (Tilden, 1958). Supplementary feeding with the normal foodplants (*Plantago erecta* Morris and *Orthocarpus* spp.) was done when possible.

As soon as pupae hardened enough to permit handling they were placed in the field. Transects were laid out in areas from which larvae had been collected (areas of relatively high larval densities). Pupae were placed directly on the soil or foliage every 25cm (my span plus 2cm) along the

transects (Fig. 1). Edgewood Park is open to the public and I wanted my transects to be inconspicuous to people as well as to potential predators, so I marked each pupa with a tiny (7 x 4mm) paper flag mounted on an insect pin. These I could easily relocate. A typed number on the flag identified each pupa. An acrylic spray (Krylon Crystal Clear 1301) applied to the page before cutting the flags out made the numbers proof against rain.

Pupae were checked every three to seven days, depending on weather conditions, and their fates were recorded as follows:

- (1) Parasitized two kinds of parasitoids emerged from pupae. One was a tachinid fly (Siphosturmia melitaeae Coquillet, determined by Paul Arnaud, Calif. Academy of Sciences) the larva of which bored out the side of the pupa and then itself pupated, sometimes near enough to be found. The exit hole was larger than that made by the piercing predators. The other parasitoid was a large ichneumonid which caused the pupae to change to an orangish hue. In emerging from an infected pupa, this wasp cut a circular cap off the top of the pupa. This cut (Fig. 2) was entirely different from the typical lines of fracture resulting from butterfly eclosion (Fig. 3). Butterflies that successfully eclosed left behind a case fractured along typical lines and very much thinner than that left by even the most thorough predator.
- (2) Stepped on pupae crushed. The evidence often included signs of trampling, showing the outline of a footprint, usually of cattle.
- (3) Died intact pupae remaining, apparently unmolested, throughout the study. They eventually either shrank and were found to be empty, or they turned black and contained a foul black liquid (probably due to a virus).
- (4) Vanished pupae not relocated, although their marking flags were. None of the traces mentioned below were found.
- (5) Predated pupae clearly damaged by one predator or another. One predator left behind ¼ to ½ of the pupal case, the inside of which was well cleaned out. Another made rough gashes (Fig. 4) and ate most of the contents, leaving the inside of the case coated with gore. Another predator or suite of predators pierced the pupal case and sucked out some or all of the contents. The damage in the two latter cases was consistent with "tasting but not eating". Related species are known to be unpalatable as adults and to a lesser extent as pupae (Bowers, 1980, 1981).

Degree Days (F.) were calculated according to Rahn (1971): [(daily max  $\leq$ 86) + (daily min >50)]/2 -50.

#### Results

Total pupal mortality ranged from 53 to 89% (Fig. 5). The major mortality factors, in order of increasing importance, were the following:

Parasitism was a minor factor, taking 1-10% of the pupae. The tachinid (Siphosturmia melitaeae) is endemic to virtually all E. editha bayensis populations, but its average infection rate is only 7.8% (45 samples from



Fig. 1. Pupa of Euphydryas editha as placed in the field.



Fig. 2. Remains of *E. editha* pupa placed in the field at Edgewood Park in 1983. Note the precise circular break made by a parasitoid as it emerged.



Fig. 3. Remains of E. editha pupa from which an adult butterfly successfully emerged. Note the thinness of the cast shell and fracture lines typical of normal emergence.

1963-1984, 407 tachinids/5212 larvae) and was only 1-2% in these three samples. Presumably the tachinid infects prediapause larvae, but death of the host does not occur until the pupal stage. Infected pupae can often be identified by their low weights. Healthy female pupae average about 380mg and males about 280mg. Tachinid parasitized pupae weigh under 200mg.

A large ichneumonid was found to oviposit in pupae in the field, a phenomenon previously undetected. The first observation was actually of a female (probably parthenogenetic) wasp palping a pupa in the field. This predatory species is probably generally unimportant, having taken 10/239 pupae in 1982, 3/160 in 1983, and 0/260 at MH in 1984 (nor did it turn up in a larger sample at MH in 1985). Since it is necessary to collect or observe pupae in order to detect it, it is not surprising that this predator is known to date only from EW.

Crushing generally was found to be a minor factor, but the large number of cattle grazing at MH raised it to 10% in the 1984 study. There are no cattle at EW and horses are supposed to be restricted to trails. Cattle were evicted from Jasper Ridge in 1960 (P. R. Ehrlich pers. comm.).

The proportion of pupae that died intact varied from 9 to 34% and apparently changed with weather patterns. The higher mortality that occurred in 1982 was undoubtedly a result of the very unusual cold and rainy weather. The number of Degree Days measured at Jasper Ridge from January 1 to March 31 in 1982 was 263, 1983 it was 353, and in 1984 it was 570. I expect that this pattern of high mortality occurs whenever late win-

ter weather is cold.

Pupae that vanished without a trace before any others in their age class had eclosed were "taken" by something, presumably a predator. Pupae disappearing while others in their age class were eclosing might have successfully eclosed and their cast cases might have blown away or been otherwise removed. This possibility could not be distinguished from removal by a predator. Here I estimated the proportion of the missing pupae to have eclosed by taking the proportion of same age class of pupae which did leave evidence of having eclosed. The remaining proportion I considered to have been eaten. The effect of this estimate is important only in the 1983 sample). Weather-delayed pupae lasted much longer than normal in 1983; 42% of them disappeared. In this unusually late year (Fig. 6) an opportunistic predator (perhaps a bird or rodent) took larger propor-



Fig. 4. Pupa of *E. editha* placed in the field at Edgewood Park, 1983, showing evidence of predation. The damage is consistent with "tasting but not eating" as might occur when a naive predator attacks an unpalatable subject.

tions of pupae later in the season. In the other two years this form of mortality was very low (Fig. 5). This temperature dependent pattern parallels that observed by Pollard (1979) for *Ladoga camilla* (Nymphalidae).

Predators that left physical remains took 23 to 32% of the pupae, making such predation the least variable factor over the three year study.

One habitat difference at MH allowed a refinement of the experimental technique used. As at any serpentine grassland site there were small areas of a fraction to several square meters in which the foliage was extremely sparse, especially due to lack of the common bunch grasses. These bare areas at MH alternated with areas of denser foliage so that my transects regularly passed in and out of them. I recorded whether pupae were placed in areas of denser foliage, bare areas, or in-between sorts of areas. Analysis of the data for MH in 1984 showed that pupal mortality varied significantly with microhabitat (G = 21.41, df = 8, P < .01; Table 2). Being crushed was more likely in barer spots (G = 8.07, df = 2, P < .025). Dying intact was less frequent in barer spots (G = 7.79, df = 2, P < .025). Neither the "eaten" group nor the "vanished" group varied significantly with microhabitat, but one might add these together as presumed predation. In that case, predation was less frequent in spots with more foliage (G = 5.992, df = 2, P = .05). Successful eclosion was not significantly better, but was nearly so, in spots with more foliage (G = 4.73, df = 2, P < .10).

Table 2. Fates of pupae placed in field at MH in 1984, according to ground cover of spot where pupae were put.

	Bare	Mixed	Dense Foliage	n
Eclosed successfully	.430	.412	.565	122
Died in place	.035	.078	.141	21
Stepped on	.158	.078	.043	26
Eaten	.237	.314	.174	59
Vanished	.140	.118	.076	29
Totals	114	51	92	257

#### Discussion

The weather of any given study is unusual and this study merely represents an extreme of that situation (Kerr, 1985). Both 1982 and 1983 were very cool, wet, and therefore late years. They differed significantly in that there were some normally sunny days early in 1982 so that development to pupation was probably normal. Then the cold set in and pupae became subject to attack by fungi and viruses. In 1983 there was an extensive period of cold, but when that ended temperatures were warm enough to allow normal pupation. On the other hand, 1984, was an extremely dry year. The rains ended very early and normal temperatures followed. Flight began and ended early (Fig. 6).

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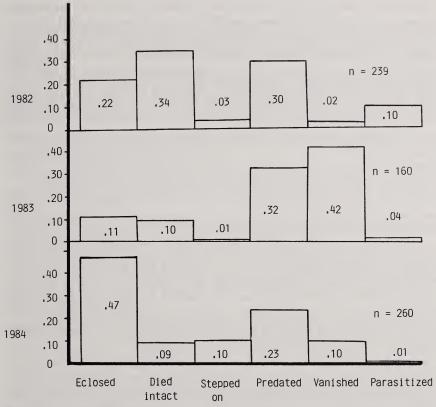


Fig. 5. Successful emergence and mortality rates by cause in three samples of Euphydryas editha pupae which were place in the field.

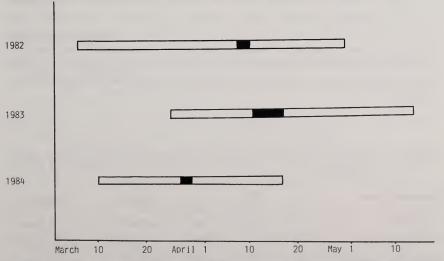


Fig. 6. Flight seasons of *E. editha* at Edgewood Park, from first to last adult seen. Shaded areas represent peak flight.

Pupation in the field took longer than expected. Laboratory eclosion is common in 10-11 days and even possible in 7 days, I had expected (in spite of Tilden's (1958) estimate of three weeks) normal field times to be about 14 days. In 1983 and 1984 field pupation periods averaged about 18 days (Table 3). The average was 27 days in the inclement weather of 1982 and many pupae (34%) died undisturbed. We have wondered for some ten years why larvae of Euphydryas editha bayensis do not break diapause earlier in the winter in order to get through the requisite life stages and enter diapause before the inevitable spring senescence of their annual foodplants (Ehrlich et al., 1975). It may be that earlier pupation would too often lead to longer, often fatal, pupation periods during cooler, rainier weather of January in the Mediterranean climate of the Bay Area.

The proportion of pupae crushed by cows at MH was great enough to suggest that this might be an important mortality factor for other life stages of the butterfly. The animal is probably not significantly exposed to this factor when diapausing or when in the adult stage. The observed fifteen day exposure of pupae resulted in a 10% mortality rate (90% survival rate), which is equivalent to .993 survival per day. Euphydryas editha probably spends about 65 days total exposed to crushing as eggs, prediapause and postdiapause larvae, and as pupae. Therefore I estimate that on the order of 35% (1-(.993)<sup>65</sup>) of the total population could be lost to crushing each generation in colonies where heavy grazing occurs.

Iwasa et al. (1983) have pointed out that pre-emergence patterns of mortality are critical in analyses of phenomena such as protandry. But the implications of the data published here (and those collected in Table 1) are of more general importance. Successful eclosion varied from 11 to 47% of the pupae placed in the field. Given that estimated adult numbers at Jasper Ridge (H and C) changed from one year to the next year by factors of 0.20 (80% decrease) to 5.00 (400% increase) in Ehrlich's twenty-five year study, this four-fold range in pupal mortality makes it clear that mortality during this stage must be estimated if we are to understand the dynamics of these populations. Leaving this as a "black box" may make any other efforts ineffective or inaccurate in explaining observed fluctuations in numbers.

Table 3. Length of pupation period in the field for *Euphydryas editha* bayensis.

Site and Year	n	$\overline{\mathbf{X}}$	s	95% CI	Range
EW 1982	47	27.0	7.02	24.9 -29.1	14-43 days
EW 1983	15	17.5	7.01	13.6 -21.4	10-26 days
MH 1984 males	52	19.9	4.38	18.7 -21.1	12-27 days
females	69	16.6	4.04	15.7 -17.6	12.23 days

#### Summary

- 1. Pupal mortality in the field was high enough in all three years to be a major factor in determining the sizes of checkerspot butterfly populations.
- 2. The pattern of pupal mortality was variable enough over time to play an important part in controlling the population dynamics of these animals; the proportion of pupae successfully eclosing ranged from .11 to .47.
- 3. Predation by predators leaving remains was the most constant portion of pupal mortality from year to year.
- 4. Other mortality factors (predation by predators that left no traces, being stepped on, and dying intact) varied greatly from one year to the next.
- 5. An ichneumonid parasitoid was found which oviposits in and emerges from pupae of the Bay Checkerspot butterfly.
- 6. Pupal mortality varies with the amount of foliage around the pupa, with more foliage resulting in less mortality from predation and crushing, but more from mold and viruses. More foliage results in a net improvement in survival rate.
- 7. Pupation in the field took 18 days under relatively favorable thermal conditions. Under colder conditions it took as long as 27 days and developmental failure was common.

Acknowledgments. I gratefully acknowledge my debt to Dennis D. Murphy, without whose cooperation this work would have been much more onerous. Paul R. Ehrlich provided access to his group's accumulated data. Irene L. Brown, Jane L. Hayes, Dennis Murphy and two anonymous reviewers provided manuscript critiques.

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#### Chromosome Aberrations in the Holocentric Chromosomes of Philosamia ricini (Saturnidae)

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**Abstract.** The nature of chromosome aberrations was studied in  $F_1$  male progeny of irradiated male parents. Translocation rings (0.34%), chains (3.7%) and fragments (15.9%) were found. Translocation chains outnumbered the frequency of rings and appear to be produced from the latter by dissociation of chiasma. Dissociation of more than one chiasmata produces bivalents and monovalents indistinguishable from the parental ones. Fragments were transmitted to the  $F_1$  offsprings stabily. Inversions were rare.

#### Introduction

Chromosome aberrations in the holocentric chromosomes usually behave in a different pattern from those in monocentrics: fragments are frequent and are stabily transmitted through several generations (Tempelaar, 1979). The nature of observed rearrangements of holocentric chromosomes in structural hybrids are, however, still doubtful (White, 1973) and to date reports on such aberrations in Lepidoptera are almost lacking. This perhaps is due to the isodiametric, numerous, much smaller holocentric chromosomes. In view of the above parameters the present study was undertaken with *Philosamia ricini* using <sup>60</sup>Co gamma ray source as the inducing agent.

#### Methods and Material

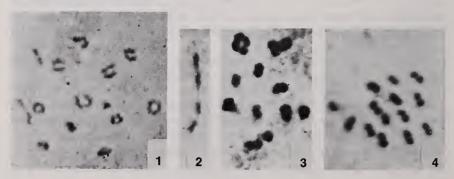
Adult males of *P. ricini*, were irradiated with an acute dose of <sup>60</sup>Co gamma ray (dose rate, 165.5 R/min.). They were held for 24 hours and then mated to virgin females. The F<sub>1</sub> male offspring were examined for meiotic chromosomal rearrangements. Cytological preparations were stained by an improved Orcein-Giemsa (OG) technique. Slides were observed and photographed using high power light microscopy.

#### Results

Spontaneous chromosome aberrations have been rarely observed in this species. However, preparations of chromosomes of the  $F_1$  male progeny obtained from the crosses of the irradiated male parent revealed the translocation rings, chains and fragments during the first spermatocytic phase

(Padhy, 1983). Chromosomal translocations of chains (Fig. 2) and rings (Fig. 3) included reciprocal exchanges of segments between nonhomologous chromosomes of the irradiated parent. These formed synapses and chiasmata, usually terminally, characteristic in the Lepidoptera (Fig. 1). Such reciprocal translocations have also been reported in the mite Tetranichus utricae (Tempelaar, 1979). Terminalisation of chiasmata was also seen in the translocated chromosomes. Terminalization of one of the chiasmata of a tetravalent ring (Fig. 3) could result in a straight chain of four (two exchanged) chromosomes with three chiagsmata intervened among them (Fig. 2). This structure is frequently noticed (Fig. 4). In the meiotic spermatocytes bearing the reciprocal translocations of the F<sub>1</sub>, the number of bivalents was reduced to 12 (n=14, Fig. 4) or less, excluding the translocation tetravalent. The translocation chains, however, cannot result from either fragmentation or differential condensation of chromatin material because such events were not observed in the gamma irradiated meiotic preparations of the male parent studied after 12, 24, 48 hour intervals (Padhy, 1983).

As is clear from Table 1, translocation chains (3.7%) were more frequent than the translocation rings (0.34%) and are thus about ten times more frequent. This result indicates a rapid terminalisation of one of the chiasmata of the tetravalent before metaphase I (Fig. 5A). Rapid terminalization of two chiasmata could give rise to two bivalents each attached by a single chiasma in between (Fig. 5B). These cannot morphologically be differentiated from normal bivalents and therefore pass undetected. The third type (Fig. 5C) indicates a chain of three chromosomes attached by two chiasma which come across in  $F_1$  meiosis. The other complement appears



Figs. 1 and 4. Normal diakinesis and metaphase I in spermatocytes.

Fig. 2. Translocation chain in a diakinesis spermatocyte of the F<sub>1</sub> male from the gamma irradiated male parent. Two exchanged and two nonexchanged chromosomes remain associated by the intervening chiasmata.

Fig. 3. Metaphase I spermatocyte of the F<sub>1</sub> male progeny of the gamma irradiated male parent. Arrow indicates the translocation quadrivalent with a chromosome complement of 13 bivalents.

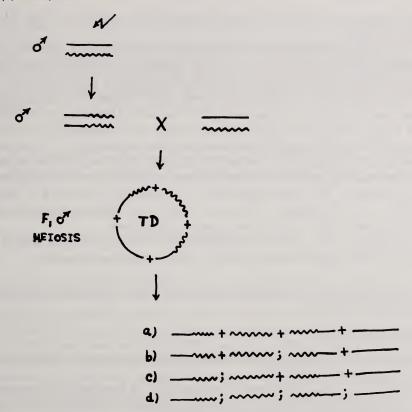


Fig. 5. Mating protocol of the irradiated male *P. ricini* crossed to a normal female. F<sub>1</sub> male meiosis indicates a translocation ring during diakinesis. This could possibly give rise to four types of chromosome associations by the chiasma: a) chains of four, b) chains of two, c) chains of three and one, and d) four univalents.

+ = chiasma points, = irradiated, TD = translocation during diakinesis

Table 1. Frequency of aberrations in the  $F_1$  male progeny of the gamma irradiated male parents of P. ricini.

Stage	Cells Observed	Translocation Rings N	Translocation Chains N	Total Translocations (%)	Fragments N
diplotene-					
diakinesis	140	2	16	12.8	24
metaphase	I 740	1	17	2.4	44
Total	880	3	33	_	68
		(0.34%)	(3.7%)		(15.9%)
Control	1000	_	_	_	-

as a fragment or univalent. An association of four univalents (Fig. 5D) is also possible.

The occasional appearance of univalents were noticed in many of the translocated spermatocytes, but these could not be differentiated from normal monovalents relative to the dissociation of a single bivalent.

The percentage of translocations was more frequent in late prophase spermatocytes than in metaphase. The reasons for this are given in Figure 5B which shows that translocations cannot be differentiated morphologically from the normal complements during metaphase I. This abnormality in the formation of chiasmata might partly be due to intragenic alterations and partly due to the absence of a centromere in lepidopteran chromosomes. The latter explanation is supported by the work of Bauer (1967) in the Lepidoptera, Murakami and Imai (1974) in Bombyx mori and Cooper (1972) in the mite Siteropsis graminum.

Fragments were, however, transmitted to the  $F_1$  structural hybrid in 15.9% of the spermatocytes (Padhy, 1983). Inversions were rare.

Acknowledgments. B. Nayak, Khallikote College, Berhampur, generously supervised this work.

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**Opinion.** Opinion is intended to promote communication between lepidopterists resulting from the content of speculative papers. Comments, viewpoints and suggestions on any issues of lepidopterology may be included. Contributions should be as concise as possible and may include data. Reference should be limited to work basic to the topic.

# Rebuttal to Murphy on Factors to the Distribution of Butterfly Color and Behavior Patterns—Selected Aspects

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In reply to Murphy's critique of my work (Jr. Res. Lep., 1985, 24:4). Since I think the scientific system ultimately decides the validity of propositions by scientific criteria, without too much attention to who holds positions pro or con, and doubt that anyone benefits from further airing of our differences, however strongly felt, on matters which I don't think have much to do with the scientific content of the book, such as why the material was published in this form rather than some other, whether the title is misleading, or why the cover is black and white, I am concerned that the most generally useful response may be none at all. (The butterfly on the cover, parenthetically, is an *Ideopsis juventa*, an oriental region danaid.) However, since Murphy proposes that he and I have basic differences about various scientific facts and scientific procedures, I will attempt to make clear my position on several points.

- 1. Murphy objects to the use of models or general schemes to explain observations as involving circular reasoning. I disagree, and think this is exactly the general function of models or general schemes in scientific reasoning—to bring order to uncoordinated observations or to offer an explanation of unexplained ones. It is true that making predictions is in effect proposing explanations for observations not yet made, but this is normally done in the circumstance that the proposed explanation appears to explain an observation similar to the one predicted, namely, when that model has already fulfilled its function. I cannot think of a way of explaining observations which does not require knowing what at least some are.
- 2. I think the definition of ecological niche given by Murphy is inadequate for butterflies because it lacks the qualifier, ". . for each stage of the life cycle." I think that a definition which says that adult butterflies and their caterpillars have exactly the same ecological niches overlooks too much, and do not see the objection to the concept of niches, or subsets of

niches, for adult butterflies. The calculations I gave did not specify either the terms of such niches, nor the number of different possible values of each term, but simply illustrated what one got if one did make certain assumptions about these. Murphy and I agree that not all loci contain all possible niches, which was the point, although (see below) we disagree on why this is so, at least in part, if the interrelated features of color pattern and preferred height of flight in the vegetation are part of the definition of the "niche" of an adult butterfly.

- 3. Although the book contains a variety of conclusions and propositions on a variety of matters, I think the single most important part is that (Chapters 1-5 and parts of others) dealing with the proposed general scheme, which relates the color patterns of the butterfly species found at a locus to the height of vegetation at that locus and the preferred height of flight in the vegetation (from the top down) of butterflies with each specific category of color patterns. The scheme addresses the fact that, as one goes north from the tropics in this hemisphere, for example (or up a mountain in the tropics), specific color patterns disappear in a sequence, with, as one goes north, transparent patterns dropping out in Mexico, tiger-stripe (orange with transverse dark stripes) patterns at about the Texas border, and black with red patterns and black with blue patterns progressively farther north, so that at about the arctic circle (or above tree line) the only species truly resident at the locus have as color patterns only relatively "pure color" white, yellow, orange, blue or lighter brown, or intergrades of these. Murphy proposes that this is due to the reduction in total number of species resident at any locus which occurs as one goes north, but I believe this is not an adequate explanation because it does not explain the systematic shift in the proportions of species resident at any locus which have specific color patterns as one does this. The question the scheme is addressing is not, "why are there fewer transparent or tiger stripe species in the United States than there are in the tropics?," for example, but, "why are there none?"
- 4. The sequence given above coincides with that given by Papageorgis in her description of the layering of flight levels of butterflies with various color patterns in amazonian forests. Murphy says her paper on this is "controversial," but not that her description of the layering is incorrect, and my own field observations in five countries in the American tropics convince me that it is correct. It is presented as fact (although without specific attribution) and illustrated by Sbordoni and Forestiero (pages 212-213), for instance.
- 5. My proposition is that the identity of these two sequences is not an accident, but reflects the workings of a specific underlying mechanism, and I supported the proposition that the sequences are what they are because selection has "geared" color pattern to height of flight in the vegetation because each pattern is most effectively cryptic at the level in the vegetation (again, from the top down) at which species with that pat-

25(1):67-70, 1986

tern regularly fly. Murphy says that I did not adequately consider the roles of "oviposition host selection and breadth, the role of nectar as a limiting resource, the use of alternative sources of carbohydrates and amino acids, thermal constraints on butterfly activities, how resources are partitioned, how butterfly diversity and plant diversity correlate and so on." I do not see that any of these necessarily make specific butterfly color patterns occur or not occur at specific loci, and do not think his list contains the mechanism. We know for instance, both that closely related species (e.g., the viceroy and the red-spotted purple) can develop both color patterns in different color classes and the appropriately different flight levels, and that males and females of sexually dimorphic species (e.g., eastern tiger swallowtail, Diana fritillary) can have patterns in different color classes. I also do not think that differences in heat-collecting capacity of different wing colors are the explanation because, for example: 1) the color pattern group most specifically associated with the deepest part of amazonian forests is the transparent one, not one of the darker ones, and; 2) the color patterns persisting in the far north are the lighter "pure color" white, yellow, orange, blue or brown ones, not the darker ones.

- 6. I think the next most important section of the book (Chapters 7, 8) deals with the points that a number of still stated criteria of mimicry systems are unnecessary, and in many specific instances not correct. These include the idea that in Batesian mimicry systems models must be more abundant than mimics in all loci, and that in Batesian systems models and mimics, and in Muellerian systems co-models (or co-mimics), must have the same ranges, because the rules overlooked the point that many birds migrate. Murphy happens not to criticize this portion of the book.
- 7. Murphy sees the data tables as a "smoke screen." Again, I disagree, because I do not think one can expect people to evaluate scientific conclusions or propositions without access to the data on which they were based. Most of the data are not mine originally, as is made clear throughout, but are derived from the publications of others, and are assuredly not generally wrong, so I think drawing conclusions from them or making propositions based on them is not scientifically inappropriate. The largest data set in the book which is strictly my own is that in the chapter on interference color patterns, which chapter Murphy happens not to criticize.
- 8. The book discusses a variety of other facts which "stick out" of the data, and offers conclusions or propositions based on them, including:
  - a) there is, overwhelmingly, a systematic relation between the color patterns of males and females of sexually dimorphic species, and the differences follow the pattern of the classes in the general scheme. If the whole thing is chance, why should this be?
  - b) the proportions of pierid and lycaenid species which have mistletoefeeding larvae decline disproportionally as one goes north from the

tropics.

c) toxic/protected papilionids are less likely than Papilio species in the same regions to show sexual dimorphism with the sexes in different color classes.

d) toxic/protected species are more likely than others to have similar color patterns on both upper and lower wing surfaces.

As regards these latter two, since intraspecific Batesian mimicry is accepted for the monarch, for instance, I don't think that what amounts to propositions that intraspecific Muellerian mimicry and, in fact, intraindividual Muellerian mimicry, also occur are particularly radical ideas, but I have never heard either one presented before. To me these again illustrate the importance of access to the data. (A possible volume two, perhaps unfortunately already over 300 pages long, contains a proposed explanation of the point on mistletoes, among many other things.)

#### **Notes**

# Field Notes on Clossiana improba harryi Ferris (Lepidoptera: Nymphalidae)

This species was described in 1984 (Ferris, C. D., Bull. Allyn Mus. 89:1-7) from specimens collected in 1982 by Jack L. Harry of Salt Lake City, Utah. Field collecting by Ferris in 1984 and in 1985 by Lisa Snyder from the Audubon Ecology Camp of the West (University of Wyoming Trail Lake Ranch), near Dubois, Wyoming, has increased our knowledge of this species with respect to its behavior and geographic distribution.

This butterfly is a denizen of remote, high-alpine areas (above 11,000′ (3355 m)) as shown in the type locality photograph (Fig. 1). It flies in early August, and was known originally only from the vicinity of Mt. Chauvenet in the Wind River Range of central-western Wyoming in Fremont Co. The type locality is situated in the Popo Agie Primitive Area of the Shoshone National Forest. C. i. harryi was described originally as occurring in eleven colonies extending for approximately 4.5 miles along the Bears Ears Trail. In 1984, I found that the distribution in this region is not discrete, but rather continuous from west of Adams Pass to west of Mt. Chauvenet. In 1985, Snyder discovered two additional colonies of harryi in the Fitzpatrick Wilderness Area at Goat Flat and Ram Flat. These localities are respectively 40 and 45 air miles NW of the type locality, also in the Shoshone National Forest in Fremont Co. Figure 2 is a map of this butterfly's range, as currently known.

The habitat of this species is in relatively level, somewhat xeric, areas of granitic



Fig. 1. Type locality (looking to the West) and typical habitat of *C. improba harryi*.

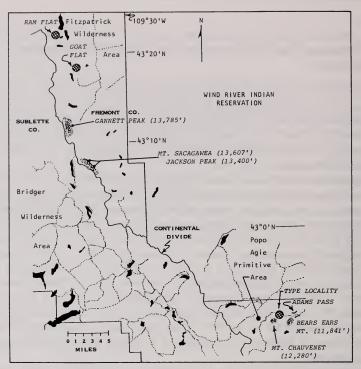


Fig. 2. Map showing the distribution (cross-hatched circles) of *C. improba harryi*. Only the larger lakes are shown. The dotted lines are hiking trails.

gravel on which mats of the larval hostplant (Salix arctica Pall) grow abundantly. This plant is widespread throughout alpine areas of Wyoming, but the butterfly is very local. Adults of harryi dorsally bask on gravel patches and on the pale granite boulders distributed over their habitat. From the rather dark aspect of museum specimens of this species, one would think that these butterflies would be very conspicuous against the pale background of the gravel and boulders. This is not the case, however, in the field. The pale central areas of the wings (dorsally) produce a cryptic pattern which blends very well with rocky substrates and renders the butterflies difficult to detect.

To date, this species has been found only on the east slope of the Wind River Range in Fremont Co., Wyoming. The eastern slope of the Range is considerably drier than the western slope which supports many butterfly fauna. It will be surprising if *harryi* is not eventually discovered in neighboring Sublette Co., at appropriate elevation, on the western slope of the Wind River Range. Access to suitable habitat areas, however, is only by foot or horseback over 20 miles or more of rugged terrain. This butterfly is abundant once a colony has been located, and is in no sense endangered, as may possibly be the case for its sibling species in Colorado *C. acrocnema* (Gall & Sperling).

Clifford D. Ferris, P. O. Box 3351, University Station, Laramie, Wyoming 82071-3351

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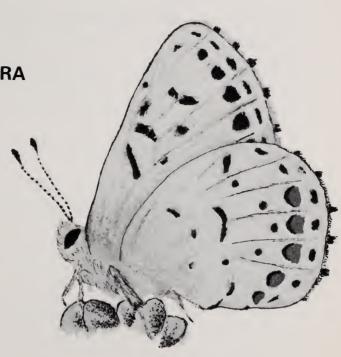
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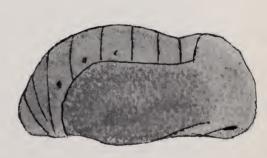
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# A New Species of *Calisto* from Hispaniola with a Review of the Female Genitalia of Hispaniolan Congeners (Satyridae)

by Kurt Johnson

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Abstract. Calisto ainigma, new species, is described from a unique holotype female collected at Jarabacoa, Dominican Republic in 1985. Female genitalia, not previously studied in Calisto, are compared for twenty-two Hispaniolan congeners. Of all congeners, wing patterning in C. ainigma only slightly resembles C. elelea Bates, a species of limited Haitian distribution. Female genitalia suggest the two may be distant sister species.

#### Introduction

The diversity of the satyrid genus *Calisto* is remarkable. With the recent work of Schwartz (1983a, 1983b, 1987 [in press]) Schwartz and Gali (1984) and Gali (1985), twenty-five *Calisto* species are recognized as occurring on Hispaniola. Eleven of these result from work of Schwartz and Gali in seldom collected areas of Hispaniola and represent endemic taxa with extremely limited known geographic ranges. This latter characteristic of *Calisto* led Schwartz and Gali (1984, p. 10) to suggest the discovery of further endemic *Calisto* from Hispaniola as inevitable. Genericly, *Calisto* are endemic to the Antilles and characterized by each of the islands exhibiting various endemic species (Munroe, 1950). Given the increasing diverity of *Calisto* taxa recognized as occurring on Hispaniola (11: Bates, 1935, 1939; 12: Michener, 1943; 14: Clench, 1943a, 1943b; Riley, 1975; 20: Schwartz and Gali [see p. 1]; 25: Gali, 1985) it may be anticipated that when adequately sampled, Cuba may also yield a diversity of *Calisto* taxa. With the appearance of

Schwartz's (1983a; 1987 [in press]) treatments of Hispaniola butterflies, an ample amount of data concerning the taxonomy and distributions of Hispaniolan *Calisto* has now been accumulated.

Characteristic of the results of Schwartz and Gali's work has been documentation that among the few cosmopolitan Hispaniolan Calisto (like confusa Lathy and obscura Michener) there occurs a number of other endemic species characterized by (a). marked wing pattern differences from the previously known congeners and slight, if any, sexual dimorphism and (b), extremely limited local known distributions often marked by restriction to a single known locality or limited habitat. The former results from the lack of comprehensive collecting prior to the work of Schwartz and Gali; the latter reflects the often extreme fragmentation of the native habitats of the island, remnants of which are now often only found in very limited undisturbed areas of inaccessible topography. This latter factor also seems to explain the lack of any recent association of specimens with the names C. montana and C. micheneri Clench (1943a, b). The holotypes of these species have been illustrated by Riley (1975) but both are from localized and remote localities from which no further specimens have been taken in recent vears.

Hitherto, all studies of *Calisto* have examined characters solely of the wing and male genitalia. Given the recent accumulation of studies of Calisto cited above, an examination of female genitalia of the group is requisite and timely. Further, such an examination has been required by the collection in the Central Cordillera in 1985 of a female specimen of Calisto (hereinafter in introduction referred to as "the Jarabacoa female") with wing pattern quite unlike any previously known taxon of the genus (Albert Schwartz, pers. comm). Matusik captured the specimen while he and Johnson were collecting along a stream near Jarabacoa, La Vega Province, Dominican Republic, June 26, 1985. A perfectly fresh specimen, it had attracted attention because amongst extremely common C. obscura and C. confusa which "flash" brown and submarginal white when flying, this specimen was markedly yellowish. Upon capture, the several unique traits noted in the following diagnosis were obvious and further heightened interest in the specimen. Unfortunately, due to pre-arranged itinerary the collectors had to leave the area that day; they returned with additional local collectors a week later but concerted Calisto collecting yielded no further examples.

Fig. 1. Female genitalia of Hispaniolan *Calisto*. Format, each entry, above: papillae anales, lateral view; below: genital plate, ductus bursae and corpus bursae, ventral view. A. *C. elelea* (AMNH), Sierra de Baoruco, 12 km. from Las Abejas on Las Abejas highway, Dominican Republic [D. R.], 400 m., May, 1984, D. Matusik; B. *C. ainigma*, holotype (AMNH); C. *C. obscura*, paratype (AMNH), Puerta Plata, D. R., 7–8 May 1915; D. *C. confusa* (AMNH), Trujillo City, D. R., 1946, A. L. Stillman; E. *C. debarriera* (AMNH), 10 km. SE Constanza, D. R., 1270 m., D. Matusik; F. *C. batesi*, same data as A.; G. *C. lyceia* Bates (MCZ), Isla Saone, D. R.; H. C. *tragia* (ASC), 1–4 km. WNW

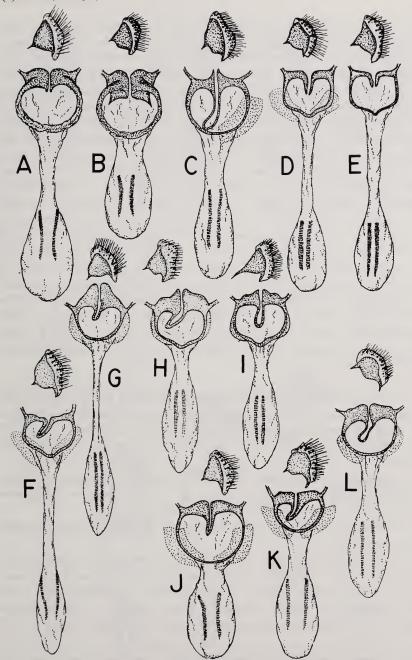


Fig. 1. (Cont). Scierie, Sud-Est, Haiti [H], 2000 m., 4 September 1984, A. Schwartz; I. *C. micrommata* (ASC), 2 km. NE Puesto Piramide 204, La Estrelleta, D. R., 1700 m., 16 July 1983, A. Schwartz; J. *C. sommeri* (AMNH), 38 km. marker, 2 km right turn to Nursery, highway to Las Abejas, D. R., 1600 m., May, 1984, D. Matusik; K. C. *hysia* Godart (AMN), Paradis, D. R., 600 m., 15 August 1932; L. *C. grannus* (ASC), 21 km. SE Constanza, La Vega, D. R., 2500 m., 10 July 1980, A. Schwartz.

The Jarabacoa female was donated to the AMNH and has since been studied in more detail, along with examination of the relevant literature, specimens from the collections of the junior author, AMNH, Allyn Museum of Entomology, Museum of Comparative Zoology (Harvard) (MCZ), Albert Schwartz (ASC) and Frank Gali, and female genitalia of Hispaniolan congeners represented in these collections (Figs. 1 and 2). There has been considerable discussion amongst students of Hispaniolan butterflies concerning the status of the Jarabacoa female considering its extremely unique wing markings and occurrence at one of the most frequently collected localities on Hispaniola. Schwartz (pers. comm.) advised that even though its markings did not seem closely comparable with any known Calisto, the specimen must be suspected as a possible aberration of either of the common local congeners. C. confusa or C. obscura. Dissection of the unique Jarabacoa female has revealed a genitalic configuration differing radically from both C. confusa (Fig. 1, D) and C. obscura (Fig. 1, C) as represented by topotypical, paratypical and syntopic/synchronic examples. In addition, the genitalia of the Jarabacoa female do resemble those of another known Calisto (Fig. 1, A) and further examination of this latter taxon has indicated certain wing pattern similarities (Fig. 3). As a result, these data suggested three alternative treatments concerning the Jarabacoa female:

- 1. Conclude from the wing pattern and genitalic characteristics that it represents an undescribed species of *Calisto* whose taxonomic position in the genus is concordant (*sensu* Murphy and Ehrlich, 1984, p. 27) with an overall view of morphological and biogeographic characteristics of the group.
- 2. Conclude by speculation that it is an aberration of some previously described species of *Calisto*, though the latter cannot be designated because of the divergent wing morph of the former.
- 3. Accord no published recognition to the unique specimen pending further sampling.

We believe that genitalic and wing character evidence assembled in this study (Figs. 1-3) along with the highly insular nature of many *Calisto* distributions warrants the first kind of treatment. We would have accepted the second treatment if the genitalia of the Jarabacoa female had resembled any geographically proximate congener. We

Fig. 2. Female genitalia of Hispaniola *Calisto*, continued. Format as in Fig. 1. A. *C. arcas* (ASC), 14 km. SE Constanza, La Vega, D. R., 2100 m., 20 July 1985, A. Schwartz (small letters referenced in text); B. *C. crypta* Gali (AMNH), Monte Christi, D. R., 13 March 1931, A. L. Stillman; C. *C. franciscoi* (ASC), 8 km. ESE Canoa, Barahona, D. R., 28 July 1985, A. Schwarts; D. *C. hendersoni* (ASC), 4 km. E El Limon, Independencia, D. R., 2 April 1984, A. Schwartz; E. *C. schwartzi* (AMNH), same data as Fig. 1, J; F. *C. clydoniata* (ASC), 2 km. NE Puesto Piramid 204, La Estrelleta, D. R., 1400 m., 13 August 1983, A. Schwartz; G. *C. galii* (ASC), 10 km. SE Constanza, D. R., 1800 m.,

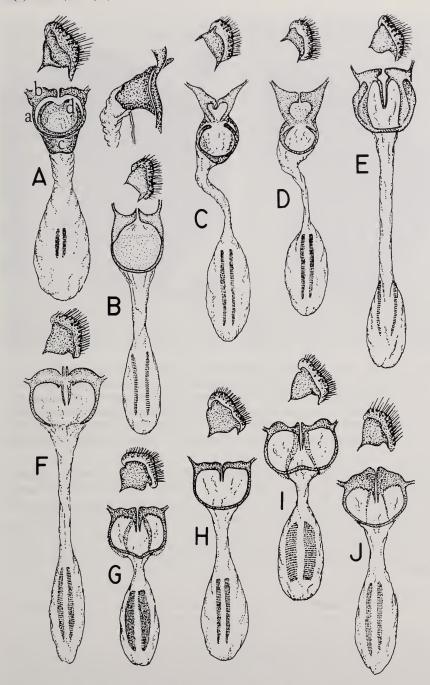


Fig. 2. (Cont). 9 July 1980, A. Schwartz; H. *C. clenchi* Schwartz and Gali (ASC), 5 km, Ne Los Arroyos, Pedernales, D. R., 1800 m., 30 June 1983, A. Schwartz; I. *C. chrysaoros* Bates (ASC), 5 km. NE Los Arroyos, Pedernales, D. R., 1800 m., 4 October 1983, A. Schwartz; J. C. *neiba* Schwartz & Gali (ASC), 15 km. S. Elias Pina, La Estrelleta, D. R., 1100 m., 26 July 1981, A. Schwartz.

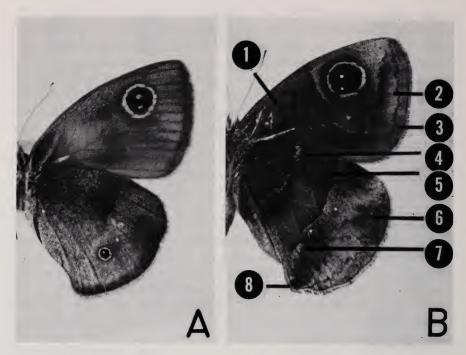


Fig. 3 Eight under surface similarities between *C. ainigma* (left) and *C. elelea* (right). 1. completely red-orange discal cell; 2. lightened apical ground color; 3. outline of marginal band (*elelea*) (fully black in *ainigma*); 4. light post-basal line; 5. darkening costad in medial area; 6. darkening costad in limbal area; 7. light mesial line extending from anal angle basad hindwing ocellus; 8. darkened spot at anal angle.

consider the third action inappropriate because (a). there has been a paucity of study of female genitalia in *Calisto* hitherto (see Remarks), (b). lack of such study has left a number of variant females cited in the literature as undetermined and (c). not recognizing the wing and genitalic features of the Jarabacoa female would result in loss of their potential taxonomic and biogeographic information as regards ongoing studies of *Calisto*. We therefore propose the following:

# Calisto ainigma, Johnson, Quinter & Matusik, new species Figs 1B, 3A, 4

**Diagnosis.** Distinguishable from all other known *Calisto* by the following marked characters: (1). undersurface ground color distinctly yellow to ochre [yellower than in photo (Fig. 4), such hues caused by differential spacing of deep brown scales amongst bright yellow scales], not brown or grey as on congeners; (2). both wing undersurfaces with wide (1 mm.) olive-black marginal band, not occurring on any congener; (3). aside from unique marginal band, hindwing lacking any bands (congeners variously have postbasal medial, postmedial and/or submarginal bands of various colors and/or a dark basal disc with its distad margin bandlike [C. montana, C. micheneri]). Rather, C.

ainigma has a yellow ground color appearing as blackish-grizzled from the wing base distad to an indistinct medial juncture with purer yellowish ground color distad in the postmedian areas to margin. Intense blackish-grizzling centered costad along this medial juncture, along with invasion basad of the marginal line in cells M<sub>1</sub> and M<sub>2</sub>, adds further oddity to the pattern; latter suffusions resemble C. elelea Bates (Fig. 3) which is otherwise banded; (4), as only in C. montana, C. micheneri, and C. tragia Bates, hindwing with single ocellus [cell CU<sub>1</sub>] devoid of any obvious surrounding patterning [not with [a]. single ocellus surrounded by various maculation expansive distad (C. confusa, C. obscura, C. hysia Bates, C. elelea, C. clydoniata Schwartz and Gali) or [b]. two ocelli, one at each end of the limbal area (C. grannus Bates, C. micrommata Schwartz and Gali, and C. sommeri Schwartz and Gali)]; C. ainigma, like C. elelea, has distinctly lighter ground color based cell CU<sub>1</sub> ocellus, in latter a band; (5). hindwing undersurface with two white dots in cells M<sub>2</sub> and M<sub>3</sub> (not with three in cells M<sub>2</sub> to R<sub>S</sub> as in C. galii Schwartz [see Remarks for further significance of this feature.

**Description.** Male. Unknown. Female. Uppersurface of the Wings: Ground color ochre-tinted olive brown, especially distad, with wings darker olive basad. Otherwise no distinctive markings. Undersurface of the Wings: Forewing ground color ochre-tinted olive with prominent subapical ocellus [diameter 2.8 mm.], black centrad, ringed yellow and with two blue-white dots within. Surrounding subapical area and adjacent postmedian area sheened lighter yellowish olive. Prominent 1 mm. olive black marginal band. Hindwing ground color yellowish-ochre; except for 1 mm. wide olive-black marginal band, without any other bands. Rather, blackish-grizzling proceeds from wing base to variously distinct medial juncture with yellow-ochre ground color distad on remainder of wing. Blackish grizzling concentrates costad along this medial juncture; marginal band intrudes basad in cells M2 and M1. Distad medial juncture of black grizzling, yellowish ground color broken only by two white dots in cells M<sub>2</sub> and M<sub>3</sub> and small but prominent ocellus [diameter 1.0 mm.] in cell CU<sub>2</sub>, black centrad, ringed yellow and with white dot within. Forewing length: 16 mm. Male Genitalia. Unknown. Female Genitalia. Fig. 1B. Of congeners studied, sharing with C. elelea (a). thickened ring of genital plate (see Remarks), ring heavily "wrapped" with membranous folds obscuring widened under-lying sclerotized ring which in other ringed taxa (see Remarks) is thinner and not heavily membranous, and (b). dorsad configuration of the ring comprised of two bilaterally symmetrical widened areas, extremely thickened and bulbous relative to congeners and which on C. ainigma shows a tapered, dorsad pointing extension. Corpus bursae markedly shorter on C. ainigma than C. elelea and with signa of former located far cephalad the juncture of this bursae with the membranous ductus bursae.

Type. Holotype, female, deposited AMNH, La Vega Province, Dominican Republic, 930 m. in central portion of Cordillera Central, June 26, 1985, by David Matusik at site characterized as follows: along a small (1.5–2.5 m. wide) stream currently running between the Hotel Pinar Dorado's group of "cabanas" and the highway that proceeds from the immediate entrance to the hotel grounds about 4 km. northwest to central Jarabacoa (which is expanding its outer perimeter by active outlying home development). Stream crosses a fenced cattle grazing break between the stands of Australian Pine which border it west along the highway and east east of the cabanas. Specimen taken in grass

along this stream about 300 meters north of the hotel and its entrance to the highway (e.g. ca. 4 km. southeast of Jarabacoa).

Remarks. Schwartz (1983a, fig. I, J) and Schwartz and Gali (1984) mention variant females which they either associate as aberrants with known *Calisto* taxa or which show facies leading them to conclude "another species of *Calisto* presumably occurs in the Cordillera Central" (Schwartz and Gali, 1984, p. 10). Concerning these, and undescribed taxa currently being described by Schwartz or Schwartz and his colleagues, Schwartz (pers. comm.) has assured us that none is similar enough to the facies of *C. ainigma* to warrant discussion here. The genitalic survey conducted during this study warrants the following general remarks.

Characters of the female genitalia apparently provide a far more useful reference for *Calisto* than those of males. Male genitalia of *Calisto*, which have been reviewed to some extent by nearly all authors cited herein, are mostly alike. Minor but consistent differences have been cited, particularly by Michener and Schwartz *et al.*, to distinguish various taxa which also have distinctive wing pattern characters. Within *Calisto*, as presently defined, the only radically divergent male genitalia amongst Hispaniolan taxa occur in *C. elelea*, *C. pulchella* Lathy, *C. arcas* and *C. raburni* Gali. As can be seen in Figs. 1 and 2, such divergence is reflected in the female genitalia of both *C. elelea* and *C. arcas*, though the former is more like other *Calisto*. *C. pulchella* is not figured becaused its female genitalia are so divergent as to suggest lack of recognizable homology with other taxa presently placed *Calisto*, a matter presently under study. *C. raburni* is recently described and its female unknown.

Two general genital plate configurations are apparent in Calisto studied, those with two obvious components and those with only one. Other taxa are intermediate between these extremes. C. arcas (Fig. 2A) best exemplifies a two component structure: a sclerotized ring (Fig. 2A, a) with a sculptured dorsal crown (Fig. 2A, b) and a sclerotized ductal tube (Fig. 2A, c) with dorsad "horns" (Fig. 2A, d). In C. franciscoi Gali and C. hendersoni Gali (Fig. 2C, D) apparent remants of these horns appear within a configuration otherwise characterized by distinct separation of the ring and crown, C. schwartzi Gali (Fig. 2E) exhibits remants of the horns closely allied with the ring and crown combination. In the remaining Calisto (Fig. 1, 2F, F-J) the ring, closely combined with the crown, forms a generalized configuration. However, within this group some taxa exhibit a sclerotized loop within the ring (Fig. 1C, F-L), or without a loop, variously developed cephalad pointing prongs (Fig. 1, A, B, D-J). The particular structure characterizing C. elelea and C. ainigma has been described in the above description. Within Calisto there are also apparent differences in the configurations of the papillae anales, ductus bursae and corpus bursae with its associated signa. It is likely that these characters will prove very useful in examining the taxonomic and biogeographic relations of the Calisto endemic to various Antillean islands. Such a study is in progress. At present it is important to note that female genitalic characters corroborate the species statuses accorded the numerous presently recognized species in Hispaniola, and particularly of interest those named very recently by Schwartz and Schwartz and Gali [see p. 1]. The only exception might be C. confusa and C. debarriera Clench which, though considered full species on biological grounds (Schwartz, pers. comm.) are very similar compared to other congeners. As regards the often debated species status of *C. hysius* ssp. *batesi* Michener (Clench, 1943b; Schwartz, 1983a; Riley, 1975), female genitalia appear to provide a moderately strong argument supporting *C. batesi*'s specificity.

The similarity in female genitalic facies of *C. ainigma* and *C. elelea* was unanticipated. The latter species has a highly insular distribution limited to montane areas surrounding Port-au-Prince, Haiti. Subsequently noted similar-



Fig. 4. Holotype female, *Calisto ainigma*, new species. Left, upper surface of the wings; Right, under surface of the wings.

ities in certain aspects of the wings patterns of C. elelea and C. ainigma (Fig. 3) are likewise suggestive and have invited the conclusion that the facies of C. ainigma is not so extraordinary as originally presumed by us and other workers familiar with Hispaniolan Calisto (e.g. Schwartz, pers. comm.). Male genitalia of C. elelea are distinctive such that among Calisto Brown and Heineman (1972, based on Michener, 1943) placed this species within a monotypic species group. It will be of extreme interest whether the male of C. ainigma, once discovered, further corroborates C. ainigma's placement with C. elelea as a sister taxon.

Etymology. The name is Greek for "enigma", referring to the curious wing pattern, occurrence at the often collected Jarabocoa area, and unanticipated suggested sister species relationship to *C. elelea*. Upon the suggestion of Schwartz and Gali (1984) and Gali (1985) species names in this paper have been made to conform to the feminine gender of the name *Calisto*. A single exception is *C. grannus*, the origin of which name Schwartz states is indeterminate.

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# Records of Prolonged Diapause in Lepidoptera

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Abstract. Previously unpublished records of diapause and adult emergence one or more years beyond that of other individuals in the species are reported for 19 species of moths in 8 superfamilies. Records of prolonged diapause are summarized, representing 90 species in 10 superfamilies. Prodoxidae, Saturniidae, Pieridae, and Papilionidae predominate, but other taxa may be disproportionately underrepresented owing to lack of study. In Lepidoptera, extended diapause occurs in prepupal larvae or pupae and is most often observed in species that live in areas of seasonal drought and in cone- and seed-feeding species that depend upon crops of erratic abundance. We do not have convincing evidence for a genetically fixed polyphenic expression, wherein a small number of individuals carryover irrespective of environmental conditions.

Prolonged diapause is the maintenance of the dormant state in insects for one or more years beyond the period of emergence by most individuals in the population. There have been many records of the phenomenon in Lepidoptera, particularly in butterflies and Saturniidae, most often originating from pupae held indoors or in climates distant from the natural ones. In the past such records were regarded as aberrant, even astonishing occurrences that had no particular biological significance. Few researchers were sufficiently interested to carry out controlled experimental research on the relationships between the underlying genetic variability and environmental factors that might demonstrate causes and possible adaptive values of prolonged diapause.

In recent years, however, a number of reports suggest that in many insects multiannual delay of development is neither anomalous nor even exceptional and that it may have important adaptive significance (e.g., Danks, 1983; Hedlin et al., 1982; Nakamura & Ae, 1977; Shapiro, 1981; Sunose, 1978; Takahashi, 1977; Tauber et al., 1986). A selective advantage of facultative carryover seems to be especially true in coneand seed-feeding species that depend upon hosts that produce seed crops of erratic abundance (e.g. Hedlin, 1967; Hedlin et al., 1982; Nesin, 1984; Sunose, 1978) and in desert insects, both phytophagous and predaceous (e.g. Ferris, 1919; Comstock & Dammers, 1939; Linsley & MacSwain, 1945, 1946; Nakamura & Ae, 1977; Powell, 1974, 1975, 1984b, present data).

Twelve years ago I summarized some examples of prolonged diapause in various insects (Powell, 1974), and that paper has been cited several times as though it was a review of the subject, but it is not. Recently two more comprehensive reviews have appeared (Sunose, 1983; Ushatinskaya, 1984). Sunose reviewed my records as well as others and tabulated 64 insect species in which the dormancy has been reported to extend more than a year. Ushatinskaya, evidently unaware of the Sunose compilation, listed a similar number, many of which had not been noted by Sunose. These include eggs of grasshoppers, first instar larvae of parasitic Hymenopera and of tachinid flies that live within sawfly or moth larvae which undergo prolonged diapause, first or last instar larvae of gall gnats, mature larvae of bees, sawflies and meloid beetles, and adults of chrysomelid beetles. In Lepidoptera multiannual dormancy is known only in prepupal larvae or pupae, although in many species diapause occurs in eggs, first or second instar larvae, or adults.

Sunose (1983) listed records of prolonged diapause in 20 species of Lepidoptera, and Ushatinskaya (1984) tabulated 14, of which 10 are additions to Sunose's total. There are a great many more instances known. Probably any lepidopterist who has reared many Papilionidae or Saturniidae is familiar with carryover pupae and emergences of the adults in later years. I have assembled a list of records representing about 90 species, including those reported here (Table 1). These have been reported in more than 60 bibliographic references and several unpublished personal communications. Even excluding the yucca moths (Prodoxidae), which are restricted to North America and for which I have scores of delayed dormancy rearings, about 65% of the records are for Nearctic species. This implies that search of Old World literature has been cursory, and that the phenomenon is known in many more species than I have compiled. In fact, it would be impossible to collect a complete list of references to prolonged diapause because often its records are buried in life history studies, reports on insects of economic concern, or in taxonomic works.

My purposes here are to record previously unpublished instances of delayed emergence in a diversity of moth taxa and to call attention to the likelihood that prolonged diapause is much more prevalent in Lepidoptera than previously supposed. For example, four of the occurrences listed below are species of Pyralidae, Geometridae and Noctuidae. These are families for which I have done only incidental rearing, and therefore one might expect records of extended dormancy to be commonplace in these taxa, yet I have seen few published. This suggests that diapause may be prolonged commonly in these large families, but students have not had sufficient patience to continue surveillance of pupae that do not develop in the first season and to test them in various artificial overwintering regimes. Diapause development is a dynamic process that takes place over weeks or months in North Temperate Zone insects, and the physiological responses to

Table 1. Taxonomic and geographical distribution of some Lepidoptera in which prolonged diapause is recorded

	No. of Species	Nearctic	Palearctic	Other	Duration (yrs)
MONOTRYSIA					
Prodoxidae	12	12			2-17
DITRYSIA					
Tineidae	1	1			1
Coleophoridae	2		2		2-3
Gelechiidae	1			1 <sup>1</sup>	1.5-2
Ethmiidae	7	6	11		1.5-4
Tortricidae	8	6	2 <sup>2</sup>		2-3
(Olethreutinae)					
Cochylidae	1	1			1
Pyralidae	3	2		1 <sup>3</sup>	2-3
Geometridae	5	3	1_	, 1 <sup>4</sup>	2-6
Lasiocampidae	1		1 <sup>5</sup>		
Saturniidae	18	15	3		1.25-7
Sphingidae	1	1			2
Notodontidae	5	2	3		1.5-9
(including					
Thaumetopoeinae)	3	2	1		2-4
Noctuidae (including	3	2	'		2-4
Agaristinae)					
Pieridae	17	7	10		2-6
Papilionidae	6	4	2		2-6

<sup>&</sup>lt;sup>1</sup> Pectinophora gossypiella (Saunders), diapause recorded in Egypt (Gough, 1916) and Hawaii (Busck, 1917). The species is believed to have originated from the Indo-Australian Region.

environmental changes are genetically variable. A stimulus that elicits successful development in one species, such as constant chilling for a certain period, may not be effective in another species or another population of the same species from a differing climatic zone or elevation, or even among all individuals within a population.

Typically, prolonged diapause involves some individuals that wait one or more full years beyond emergence of their sibs, in populations in which all individuals enter dormancy, for one of three life cycle patterns: a) vernal feeding followed by 9 or 10 months dormancy; b) vernal feeding followed by a few months aestivation and autumnal flight, as in *Hemileuca* (Comstock & Dammers, 1937, 1939; Ferguson, 1971), or c) facultatively double-brooded populations such as in *Ethmia semilugens* (Z.) (Powell 1974) and *Anthocharis* (dos Passos & Klots, 1969; Shapiro,

<sup>&</sup>lt;sup>2</sup> Includes *Cydia pomonella* (L.), which probably is introduced from the Palearctic (observed by several Nearctic workers and in Yugoslavia).

<sup>&</sup>lt;sup>3</sup> Loxostege frustralis Zeller (Pyraustinae), recorded in South Africa by Broodryk (1969).

<sup>&</sup>lt;sup>4</sup> Adults of the Australian species *Arhodia* (?)retractaria Wlk. (Ennominae) were reared after 21–23 months in diapause (McFarland, in litt.)

<sup>&</sup>lt;sup>5</sup> Family but no species mentioned by Danilevski (1951) in Russia.

1981), so that either a few weeks or nearly a full year in diapause elapses. I also include examples in Tineidae and Cochylidae in which individuals may wait one year even though sibs have emerged within a few days, apparently without undergoing any diapause. The potential for such species to wait more than one season seems likely.

### **Rearing Methods**

Foliage-feeding larvae usually were held in transparent polyethylene bags lined with folded paper toweling to absorb moisture and provide a substrate for cocoon construction. If the host plant material was exceptionally susceptible to excess moisture and decay problems, or the moth species were suspected to use soil for pupation, the lots were placed in translucent plastic boxes or one-gallon tubs with a few cm of sterile sand. Thus natural photoperiod normally was available. Prodoxids were housed in subdued light, in sealed cardboard boxes with a 32-mm emergence aperture at one end. During 1964–1970 most of the initial rearing was conducted in a temperature controlled lab (20–25°C) with variable humidity (RH 38–48% in dry weather, 52–78% during rainy periods). Since 1971, the active larval lots have been handled in a mobile trailer lab on the University of California, Berkeley, campus. Here minimum temperature was controlled (usually 15–16°C) but not maximum, and humidity varied with outside air conditions.

Temperature and relative humidity were recorded continuously by Bendix-Friese hygrothermographs placed on the lab shelving or in temperature cabinets with the collections or in a weather shelter located near outdoor cages. During the emergence season, moths were harvested daily or at 2-3 day intervals. Prodoxids that failed to remain in emergence vials and died inside boxes were harvested at irregular intervals and at the end of each season.

Rearing lot numbers. — A number-letter designation was assigned to each collection of one or more larvae. It reflects the year and month in which the collection was made (e.g., JAP 70C8 refers to the eighth lot recorded in March 1970). The number accompanies all associated material, including reared moths and parasitoids, preserved larvae and other artifacts such as pupal shells, and the data in notebooks. The habitat, hostplant, behavioral, emergence, and preservation data are summarized in a d-Base II program. Voucher specimens and associated data are deposited in the Essig Museum of Entomology, University of California, Berkeley.

Overwintering regimes. — At the end of each season, usually in October or November, lots known or suspected to contain carryover larvae or pupae were exposed to one or a combination of two, storage methods used to manipulate winter temperature conditions:

1. Laboratory: A constant temperature ( $20^{\circ}\pm1^{\circ}C$ ), low humidity (40-60% RH) room on the U.C. campus, was used for control sublots in

studies of prodoxids. Other overwintering lots sometimes were left in the mobile trailer lab, which was unheated for 6 weeks in midwinter during 1976–1979.

- 2. Berkeley cage: Many collections were exposed to natural winter temperature and humidity in outdoor screen cages at the Oxford Tract, U.C. Berkeley. Cages were provided with a roof, but in windy storms the containers received direct moisture. Temperatures are moderate at this coastal station, and did not fall below 0°C during several winters monitored. Weekly means of daily maximum and minimum temperatures remained above 10°C during most of the winter. RH fluctuated daily and seasonally, generally between 50–80% in dry weather, 65–95% during storms.
- 3. *Refrigerator*: A kitchen refrigerator without precise temperature monitor  $(4^{\circ} \pm 1.5^{\circ}C)$  was used for chilling during part of the winter in a few instances.
- 4. Russell insectary: An unheated, fully ventilated lab at the U.C. Russell Reserve near Lafayette, CA, was used to expose prepupal larvae to uncontrolled winter temperatures and humidity. The site is situated ca 10 airline km inland from San Francisco Bay, in the Briones Hills at ca 250 m elevation. Temperatures frequently dropped below freezing and weekly means of daily maxima and minima ranged ca +6°C to 11°C in mild winters, -4°C to +7°C in colder winters. These are much colder conditions than at Berkeley. For example, average monthly mean temperatures at Russell in 1971-73 ranged from 4.5°C lower in October to 8.5° and 7.4° lower in December and January than the 20-year average at Berkeley.

#### **PRODOXIDAE**

Prolonged diapause is documented in most yucca moths (Koebele, 1894; Powell, 1984a, 1984b; Powell & Mackie, 1966; Riley, 1892). I have recorded emergences of adults following multiannual dormancy in the prepupal larvae of Parategeticula pollenifera Davis, and in nearly all the species of Prodoxus and Agavenema. Larvae of Tegeticula have been observed to survive more than one season; Riley (1892:117) noted that a large percentage fail to complete development in the first year, with some of the moths "not issuing until the second, third of fourth year," but he did not give specific data or report conditions of overwintering. I carried out extensive tests with 4 *Prodoxus* species associated with Yucca whipplei in California and Y. schottii in Arizona over a 20-year period. The larvae of these species commonly remain in diapause 4-8 years in artificial conditions even though neighbors in the same plant complete development in a prior year. Mass emergence of a whole colony may wait 6 years, if exposed to constant temperature, but mortality was significantly higher as compared to year IV (Powell, 1984a); and in one instance mass emergence occurred after 16 and 17 years in diapause (Powell, 1985, unpubl. data).

Diapause development in *Prodoxus aenescens* Riley and *P. cinereus* Riley is a complex and dynamic process, responding to gradually changing temperatures, probably coupled with moisture factors. Larvae held in constant temperature (± 20°C) and natural photoperiod throughout winter, or exposed to constant temperature chilling (0° to 9°C) for 50 days, remain in diapause, while refrigeration in constant darkness in gradually decreased (6 weeks), then gradually increased (7 weeks) temperatures at means of 3° to 10°C induced varying proportions of individuals to develop (Powell, unpubl. data).

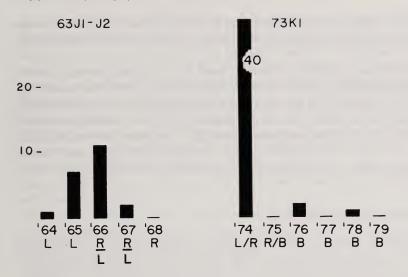
The following records are for species that have not been extensively studied and originate from localities distant from Berkeley, characterized by extremely different seasonal climates from those the larvae were exposed to in rearing.

# Prodoxus quinquepunctellus (Chambers)

This species is widespread, from Arizona eastward, in association with an array of yuccas in the Sections Sarcocarpa and Chaenocarpa (Davis, 1967). Larvae were reported by Riley (1892) to sometimes remain in the dry floral stalks 2, 3, or 4 years, although apparently he did not observe successful development of carryover individuals. I obtained delayed emergences of *P. quinquepunctellus* from three collections taken in Arizona and New Mexico, the latter over 4–5 year periods. In contrast to California species of *Prodoxus*, some individuals developed even when held in constant temperature.

The first material, consisting of stalks thought to be two species of Yucca, possibly intermedia and glauca, was collected in late September, 1963, 5 km W of Albuquerque, Bernalillo Co. by J. A. Chemsak (JAP 63J1–J2). A sample of 24 larvae was removed for preservation. The remainder were held in constant temperature through the following two seasons, and diapause development occurred in 7 individuals, one in 1964, 6 in 1965. In November, 1965, half the stalks were transferred to the Russell insectary, where winter III elicited emergence of 5 P. quinquepunctellus in 1966. During the same season, the remaining stalks in the lab produced 6 moths; one more emerged from them in 1967. Thus, development of one or more individuals took place each year in the lab, 73% of those that emerged (fig. 1). Moths eclosed in April, 1964, and March to early May in 1965, approximately coincident with the flight period in the Albuquerque area (Davis, 1967).

A second New Mexico collection was made near Portales, Roosevelt Co., in late October, 1973, by N. M. Jorgenson (JAP 73K1), and consisted of current year stalks of *Yucca glauca*. These were held in my lab until December 1, then at the Russell insectary over winter, and 40 *P. quinquepunctellus* responded in diapause development in 1974. In midwinter, 1974–75, a sample of 12 carryover larvae was removed for preservation, and the rest of the lot was moved to the outdoor cage at



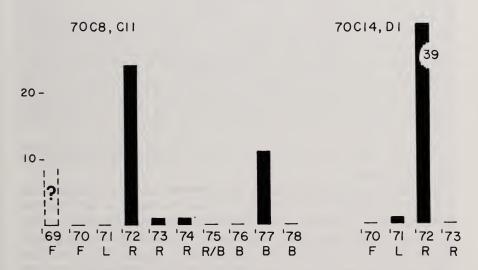


Fig. 1 (upper): Successive annual numbers of *Prodoxus quinquepunctellus* (Chambers) that emerged from two collections of yucca inflorescence stalks (see text for data).

(lower): Successive annual numbers of *Prodoxus coloradensis* Riley that emerged from four collections of *Yucca schidigera* inflorescence stalks from the Mojave Desert (see text for data).

Overwintering sites: F, in field; B, Berkeley, outdoor cage; R, Russell Reserve, unheated insectary; L, laboratory at 20 ± 2°C.

Berkeley, where it was stored for 5 years. Three additional moths emerged, 2 in 1976 and one in 1978, after 3 and 5 years in diapause (fig. 1).

One additional stalk was collected from *Yucca angustissima*, 1 km W of Cottonwood, Yavapai Co., AZ, 30 July 1970, by R. E. Dietz and P. A. Rude (JAP 70G35). It was retained in the lab for one year, during which no moths emerged, then transferred to the Russell insectary. There 26 *P. quinquepunctellus* successfully completed development, 30 May to 20 June 1972, following the second winter. Only one flaccid-appearing larva was discovered by splitting the stalk at the end of 1972.

# Prodoxus coloradensis Riley

This species feeds in stalks of *Yucca schidigera* and *Y. baccata* in California and in other yuccas of the Section Sarcocarpa in the western U.S. (Davis, 1967). Collections made in the Mojave Desert, 31 March – 2 April 1970 (Dietz & Powell), indicated that prolonged diapause in natural populations is commonplace in that habitat.

At a site 8.5 km north of Cottonwood Springs, Joshua Tree National Monument, Riverside Co., CA, Y. schidigera was in full to late bloom on March 31, and none was seen with newly emerging inflorescences. P. coloradensis adults were numerous, yet there appeared to be no 1969 stalks. Dry stalks in the vicinity appeared to originate from 1968; each had emergence holes along with few to many carryover larvae (JAP 70C7-8). Because adults of P. coloradensis had already emerged, it could not be inferred with certainty that the observed stalks were older than one year. It was evident, however, that either a substantial portion of larvae had carried over from 1968 or a previous season, or that many 1969 larvae had not completed diapause development for the 1970 season.

At Belle Campground, 32 km to the northwest and 300 m higher than Cottonwood Springs, Y. schidigera showed no signs of inflorescence development. Flowering and yucca moths had been observed at this site in mid-April, 1963, and it was evident that activity would not begin before mid to late April in 1970. Again, there appeared to be no 1969 stalks, while those from a previous year contained old emergence holes along with carryover Prodoxus larvae (JAP 70C11), which tended to confirm our estimate of stalk age at Cottonwood Springs. On the basis of weathered appearance of the stalks, subsequent vegetative growth, and lack of prior emergences, Y. schidigera stalks at Ryan Mountain, Joshua Tree Natl. Mon. (JAP 70C14) and Cedar Canyon, 27 airline km NE of Kelso, San Bernardino Co., CA, (JAP 70D1), also were judged to be more than one year old.

The 1970 collections were housed at the Russell insectary beginning in early April, and no *P. coloradensis* emerged in 1970, nor in 1971

after transfer to the constant temperature lab over winter 1970–71. Most moths (82%, n=78) completed development in 1972, following their first overwintering at the Russell insectary. Additional larvae were discovered in 70C11 in February, 1974; the lot was retained and exposed to winters in the cage at Berkeley. Only 2 adults completed development in the succeeding 2 years, then, inexplicably, 11 *P. coloradensis* (38% of the Belle Campground total, n=29) emerged in April 1977, following a second full winter of drought conditions in Berkeley, 9 years after their larval feeding in 1968 stalks (fig. 1).

It is possible that the 70C14 and 70D1 collections, which originated from higher or more northern sites than Belle Campgound, were made sufficiently early (e.g., 4 or 5 weeks ahead of flowering) that development was interrupted; but negative results of all other 1970 collections including those of *P. sordidus* Riley (see below) and *P. y-inversus* Riley (Powell, 1985) suggested that the 1969–70 winter was one that failed to elicit diapause development in Mojave *Prodoxus* generally.

Evidence of 1969 failure in the Y. schidigera inflorescence crop was dramatic at a site on Black Canyon Road, south of Cedar Canyon. Here an extensive stand of tree-like Y. schidigera possessed 1969 stalks that were dry, hard, and black, atrophied before they were fully grown, as though they were killed by a late freeze. None had any signs of lepidopterous larval feeding. A number of 1968 stalks were found containing small numbers of larvae; some had emergence holes left by sibs that must have faced catastrophe in 1969. A collection (JAP 70D4) of the pre-1969 stalks produced no adults in 1970 and only one P. coloradensis in 1972 after overwintering at Russell. Dissections of the stalks in early 1973, however, revealed a few larvae still in diapause.

# Prodoxus sordidus Riley

Moths treated under this name are believed to represent two species (D. S. Frack, *in litt.*) associated with Joshua Tree, *Yucca brevifolia*. It appears that a species with tan forewings feeds in the inflorescence scapes, while a whitish moth originates from larvae in pods. However, some of my stalk-inhabiting larvae produced the pale morph, and more information is needed to confirm separation of larval feeding niches of the two. My rearing data are pooled.

Collections at Antelope Valley, 33 km E Gorman, Los Angeles Co., CA, March 11, 1963 (Chemsak & Powell, JAP 63C8) just ahead of the current season flowering, confirmed that prolonged diapause occurs — most emergences took place in late March and early April, 1963, but 2 *P. sordidus* completed development in February, 1964 after storage in the lab. A midwinter collection from 5 km SE Pinon Hills, L. A. Co., 23 December 1969 by P. A. Opler (JAP 70A1) produced only 6 adults after housing in the lab for the remainder of the season. None emerged in 1971 after winter II in constant temperature, but in 1972, 90 moths

responded to winter III at the Russell insectary. Three more individuals waited until 1973, following a second winter at Russell, and one P. sordidus emerged in the 6th season, after the material was transferred to Berkeley in midwinter 1973–74.

The same emergence pattern was shown by population samples made 31 March - 2 April 1970 in the central Mojave Desert, despite the fact that they were collected after a full winter in the field. One of these (JAP 70C12) at Belle Campground, Joshua Tree Natl. Mon., Riverside Co., CA, was made while Y. brevifolia was in full bloom and Prodoxus was active in low numbers. It was not possible to judge stalk age precisely, but it appeared at least two seasons growth contained larvae in diapause; none of these matured in 1970. Three more collections were made at higher, more northern sites, ahead of 1970 Y. brevifolia flowering (70D2: Cedar Canyon, 27 airline km NE Kelso, San Bernardino Co., CA: 70D10: 6 km S of Barnwell, 44 airline km NE Kelso: 70D24: Kyle Canyon, 15 km W Highway 95, 30 airline km WNW Las Vegas, Clark Co., NV). In each sample, no P. sordidus matured in 1970, nor in 1971 following a year in the constant temperature lab. Most of the emergence (84%, n=140) occurred in year III following overwintering at the Russell insectary in 1971-72, while 6 individuals eclosed in each of the next two years after another winter at Russell and at Berkeley from midwinter 1973-74. Only one of the collections (70D10) was retained beyond the 5th year, and 10 P. sordidus developed successfully in 1975 after storage over winter in the outdoor cage at Berkeley, but none matured in the 7th season (fig. 2).

Prolonged diapause would seem less critical to continuity of populations in *P. sordidus* than in other *Prodoxus* because *Yucca brevifolia* blooms more consistently. Nonetheless, combined with observations of *P. coloradensis*, the data indicate that certain winters are suboptimal to diapause termination in *Prodoxus* in widespread areas of the Mojave Desert.

Weather records from Twentynine Palms (15 airline km N of Belle Campground, at 610 m) and Mountain Pass (35 air km NNW of Cedar Canyon, at 1450 m) for the preceding 4 and 3 years, respectively, showed that the 1969–70 winter was unusual, if not exceptional in a long-term sense. At both stations the rainfall total for October through March was lower than in any of the preceding few years, 19 mm contrasted to a 5–year average of 45 mm at Twentynine Palms, and 50 mm vs. a 4–year average of 92 mm at Mountain Pass. Possibly of greater significance to the moths, the 1969–70 winter was characterized by unusually mild temperatures. In the 13–week midwinter period, December through February, monthly means averaged 11.1°C at Twentynine Palms in 1969–70, contrasted to a range of 8.5–10.9° (avg. 9.9°) during the preceding 4 winters; while at the higher station monthly means averaged 7.0°C in 1969–70, but ranged 3.1 to 6.7° and averaged only 4.8° during the preceding 3 seasons.



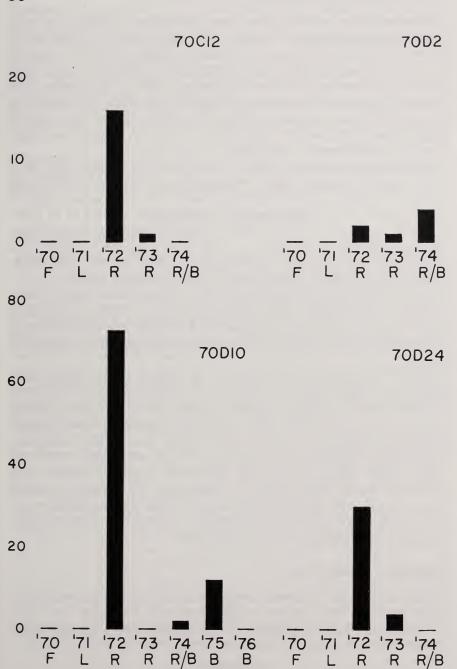


Fig. 2: Successive annual numbers of *Prodoxus sordidus* Riley that emerged from four collections of *Yucca brevifolia* inflorescence stalks from the Mojave Desert (see text for data).

Overwintering site designations explained under figure 1.

## Agavenema barberella (Busck)

Agavenema species feed on Agave and display larval habits similar to those of stalk-inhabiting *Prodoxus*. The adults are not found in the flowers of the larval host, as are *Prodoxus*, and larvae usually occur in the main scape well below the inflorescence. Collections were made from various species of Agave in Arizona in 1968–1970. Stalks were housed at the Russell insectary in 1968–69 and 1969–70 winters, in the lab 1970–71, returned to Russell in 1971–72 and not retained beyond the fourth season. Development occurred irrespective of the kind of artificial winter conditions.

Lots collected at Madera Canyon, Santa Rita Mts. in June 1968, prior to the current season flight, from *Agave palmeri* (JAP 68F43–44) (Opler & Powell), produced moths primarily the same season (83% of those reared, n=130). Emergences occurred from 15 July to 13 October, and 20 larvae were harvested in late September. Only 7 individuals completed development in 1969, after exposure to winter II at the Russell insectary, followed by none in 1970 and 1971, yet 15 *A. barberella* emerged in the 4th season after storage at Russell.

Larvae were collected in *Agave schottii* at Molino Basin, Santa Catalina Mts., in September, 1969, after the summer activity period (JAP 69J10). Small numbers of moths issued, 5 in 1970, 3 in 1971 (following a lab winter), and 7 in 1972, after winter III at Russell (47% of the total, n=15).

Lastly, 7 collections of one-year old or current season stalks were made from 3 *Agave* species in central and northern Arizona, <sup>1</sup> 29 July to 2 August, 1970. All yielded similar results: one or no moths in 1970, modest numbers in 1971 (19% of the total reared, n=134), despite having overwintered in the lab, followed by most of the emergence (78%) in the 3rd season after exposure to winter at Russell in 1971–72.

The normal flight period of *A. barberella* is poorly known, with scattered records from March to September in southern Arizona (Davis, 1967). The flowering phenology of most agaves probably enables a more protracted activity season by *Agavenema* within populations than is characteristic of yucca moths.

# **Agavenema pallida** Davis

This species, which is closely related to the preceding one and may be a geographical race, occurs in the deserts of California and Baja California Norte, Mexico (Davis, 1967; UCB specimens). Its seasonality is more restricted than that of *A. barberella*, similar to the California

<sup>&</sup>lt;sup>1</sup>JAP 70G30: 4 km E of Peach Springs, Mohave Co., 1969 stalks of *Agave utahensis*; 70G31: same data, 1970 stalks; 70G32: 5 km SW Mingus Mtn. summit, Yavapai Co., 1969 stalks of *A. parryi*; 70G33: same date, 1970 stalks; 70G36: Molino Basin, Sta. Catalina Mts., Pima Co., 1969 stalks *A. schottii*; 70H6: same data, 1970 stalks; 70H5: 1.5 km NE of Colossal Caves, Pima Co., 1970 stalks *A. schottii* (R. E. Dietz, J. Powell and P. A. Rude).

species of *Prodoxus*. Collections from *Agave deserti* in March, 8 km E Jacumba, San Diego Co., CA (JAP 63C31) and April, 1963, Pinyon Flat, 29 airline km SE of Idyllwild, Riverside Co., CA (JAP 63D10) revealed prolonged diapause. Carryover larvae remained at the end of the season, and in 63D10 a few adults emerged in 1964 and 1965 despite housing in the lab during the preceding winters.

Two collections made in Baja California in March, 1972 and 1973, yielded A. pallida adults in diminishing numbers in years I, II, and III. A total of 25 moths emerged in year I following overwintering in the field (51%, n=49), 17 in year II (35%), and 7 in year III (14%), and 2 carryover larvae were discovered in winter IV (JAP 72C12: 8 km E of E1 Rosario, 1971 stalk of Agave shawii; 73C5: 5 km S of Rancho Santa Ynez, 1972 stalks of A. cerulata spp. ?nelsoni; Doyen & Powell).

## TINEIDAE: SCARDIINAE

# "Scardia" cryptophori (Clarke)

This large gray tineid is widespread in montane western North America. It was transferred from *Morophaga* H.-S. to the genus *Scardia* Tr. by Davis (1983), who treated *Morophaga* and its Palearctic type species as a synonym of *Scardia*. However, *S. cryptophori* is structurally and biologically dissimilar from Nearctic members of *Scardia*. In contrast to other Scardiinae and other fungus-feeding Tineidae, this species is host-specific, feeding in the sporophores of *Polyporus* (*Cryptophorus*) volvatus, which grows on recently dead conifers (Lawrence & Powell, 1969). This fungus is available throughout the season but appears to be in a fresh state preferred by *S. cryptophori* primarily in spring following winter precipitation and snow melt.

Among numerous collections from the Sierra Nevada and Cascade Ranges in California, two from Trinity County produced some larvae that proceeded to maturity without dormancy, as most do, and others that entered diapause for one year. This suggests that adverse condi-

tions, particularly desiccation, may prolong diapause.

Four collections of sporophores were made in the vicinity of Hayfork, Trinity Co. in late May, 1973. Moths (n=36) emerged from all 4 lots 15–25 June, but in two groups (JAP 73E46, E47) a number of larvae spun cocoons in dry spots remote from the fungus, and most of these did not emerge. A few cocoons were cut open in September, revealing carryover prepupal larvae. The lots were stored in boxes at the Russell insectary. After removal to Berkeley in early June, 1974, 10 *M. cryptophori* emerged in late June, one year later than their sibs.

#### **ETHMIIDAE**

# Ethmia plagiobothrae Powell

This species flies in early spring, primarily in March, in the foothills of the Coast Ranges and Sierra Nevada in California. The larvae feed on

flowers of Plagiobothrys (Boraginaceae) a spring annual, and pupae remain in diapause from the beginning of the dry season until early spring the following season. I have made numerous collections of larvae, but they are highly susceptible to disease in rearing, and the few adults obtained emerged after one year (Powell, 1971). In one instance (JAP 69D58, Powell, 1971) 10 E. plagiobothrae were reared after one winter (100% of the emergence) even though the collection data and rearing conditions were essentially the same as for a collection of the closely related species, E. scylla Powell, that produced moths 2, 3 and 4 years after pupation (Powell, 1974). In another collection (13 km SE Three Rivers, Tulare Co., 4 May 1979, JAP 79E24) all 4 adults emerged the next year, between Feb. 14-27. On two occasions, however, pupae were still healthy appearing during the second winter, after 19 and 21 months, but development did not take place (Powell, 1971). Thus it was not surprising that a collection in 1980 produced one E. plagiobothrae that delayed until the second spring before emerging.

We found larvae on *Plagiobothrys nothofulvus*, 6 km S of Rough and Ready, Nevada Co., CA, on 4 May 1980 (M. Buegler, J. DeBenedictis & Powell) (JAP 80E17). About a dozen were placed in pill boxes, 2 to a container with inflorescences and folded tissue paper. After cocoon construction the boxes were left open inside a translucent plastic box, stored in the mobile trailer lab at Berkeley through the summer. In October they were moved to the outdoor cage, but no development resulted after the first winter. In 1981–82 the material was again exposed to winter in the cage, and one male emerged between 24 February and 24 March, 1982. Other individuals were unsuccessful in pupation, succumbing either to disease or desiccation prior to or after

cocoon construction.

# Ethmia epileuca Powell

This species was described from the Panamint Range, CA, in the northern Mojave in 1959 and subsequently has been recorded in the low deserts of southern California, Baja California, and Arizona (Powell, 1973; UCB specimens). The foodplant, an annual *Phacelia*, was discovered in 1977, and the one specimen reared spent two years in diapause.

A few *Ethmia* larvae were found feeding externally on *Phacelia crenulata* (Hydrophyllaceae) at Zzyzx Springs, near Baker, San Bernardino Co., CA, 20 April 1977 (JAP 77E94). They were provided with soft paper toweling, but only one *E. epileuca* successfully constructed its cocoon. It was stored in a transparent plastic bag in the mobile trailer lab through summer and fall, then in an outdoor cage at Berkeley during late winter and spring, 1978, but diapause development did not occur. The cocoon was again placed in the cage for the 1978–79 winter until mid-February, then in the mobile lab. A female

*E. epileuca* emerged on 2 April 1979 after nearly 24 months in diapause. The 1978–79 winter was appreciably colder than the preceding year at Berkeley, 190 heating day degrees greater (based on 18.3°C), during October through February.

Interestingly, a related species, *E. semilugens* (Z.), which has the capability of developing with a short diapause of a few weeks, of one year, or of several years (Powell, 1974), also feeds on *Phacelia crenulata* (Powell, 1971). Collection records for *E. epileuca*, however, indicate that this species has a univoltine cycle with flight in early spring.

## Ethmia (Macelhosiella Group) n. spp. A, B

Larvae that proved to be two undescribed species which are structurally and biologically similar to *Ethmia geranella* (B. & Bsk.) were discovered in western Fresno County, CA in March 1975 and collected again in April 1978. Both species feed in spring, estivate as pupae, and fly in late fall, as do other members of the Macelhosiella Group. Eggs hibernate, presumably in diapause or a temperature-dependent quiescence (Powell, 1973). In both Fresno County collections, some individuals carried over to a second or subsequent autumn; however the pattern was quite different between the two species, even though they were reared and held over winter in identical conditions.

Species A: The larva is green with faint longitudinal, gray integumental shading. The adult is a whitish moth with faint ochreous along the discal cell, and it differs from other western species of the group by lacking a hindwing costal penicillus in the male. P. A. Rude and I collected larvae on *Phacelia tanacetifolia* (Hydrophyllaceae) at the Ciervo Hills, 29 airline km SE of Mendota, Fresno Co., CA, 16-18 March 1975 (JAP 75C1) and at Jocalitos Cyn., 9 airline km S of Coalinga, Fresno Co., 17 March 1975 (JAP 75C2). Larvae were placed in translucent plastic vials and cardboard pill boxes, 1 or 2 per container, with folded tissue and small blocks of yucca scape pith, into which they burrowed for cocoon construction. Others were confined in translucent plastic bags with paper toweling and hostplant material. They were stored in the mobile trailer lab at Berkeley for the remainder of spring and early summer; in late July about half the containers were moved to the Russell insectary, while the remainder were placed in the outdoor cage at Berkeley in September.

Most of the moths (n=25) emerged in October, 1975. The carryover cocoons were exposed to winter conditions at Russell during January – April, 1976, and subsequently were retained in the outdoor cage at Berkeley. Two adults completed development in October, 1976, and 13 others developed but were trapped in the cocoons and unable to distend the wings, probably in the first season. No more emerged in 1977 or 1978.

In early April, 1978, following the 1975–77 drought, Jocalitos Canyon

was again a sea of wildflowers, and we made additional collections of the two *Ethmia*. Larvae of Species A (78D12) became diseased and most were preserved for taxonomic study; 7 were retained in translucent plastic boxes with paper toweling and yucca blocks in the mobile trailer lab. Four of these emerged as adults 25–30 October 1978. The remaining 3 carried over and eclosed 10–27 Oct. 1979, after storage over winter in the outdoor cage at Berkeley.

Thus 29 of 34 successful emergences (85%) of Species A occurred during the first fall after larval feeding, while the remainder developed one year later.

Ethmia Sp. B: The larva is irregularly mottled, predominately gray, with longitudinal bands of orange dorsally and laterally, resembling that of *E. charybdis* Powell (Powell, 1971). The adult is dark gray; the forewing has a trace of ochreous and a variable black line along the discal crease and a whitish dot at the end of the discal cell, and the male hindwing has a costal penicillus. Thus the adult is structurally quite similar to that of *E. timberlakei* Powell, which feeds on *Phacelia ramosissima* in southern California, but the larva of the latter is green with a yellow dorsal stripe (Powell 1971). Larvae of Species B were mixed with those of Species A in the field at Jocalitos Canyon in March, 1975, but were outnumbered ca. 10:1. I could not detect a spatial differentiation on the plants; both fed within the scorpioid floral spikes. In the lab, larvae were segregated by color and handled in the same rearing conditions as outlined for Species A.

In marked contrast to the preceding species, no individuals of Species B completed development in 1975. Instead, all 4 moths that metamorphosed did so after carrying over, two in early November, 1976, and one each in November 1978 and 1979. The same diapause behavior obtained in the April 1978 collection at Jocalitos Canyon: about a dozen larvae were confined, of which none developed in 1978, 2 moths emerged in October 1979, none the following year, and 2 more in October, 1981, after 42 months in diapause.

I visited the Jocalitos Canyon site on 21 March 1977, following two drought years in California, and found the spring vegetation dry; there had been essentially no germination of annuals. Hence, a large larval eclosion of *Phacelia*-feeding *Ethmia* would have been mostly doomed, and if prolonged dispause in the pupal stage acts as a buffer against such disasters, the strategy must be keyed to maintenance of diapause through autumn preceding a dry spring.

Adults of Species B were taken at blacklights at Jocalitos Canyon on 10 November 1977 (Powell & Rude). There had been no heavy rains in the region that fall, only ca 6 mm in the Fresno area, less than 1/4 the normal, by early November; the drought did not end until late November and December, 1977. This leaves unanswered the question of how prepupal larvae appraise the potential for spring growth of annual *Phacelia* and either maintain diapause or undergo development in October.

## TORTRICIDAE: OLETHREUTINAE

# Grapholita vitrana (Walsingham)

Grapholita vitrana was originally described from northern Oregon, and it is commonly associated with Astragalus (Fabaceae) in sandy situations along coastal areas of California, on San Miguel and Santa Catalina Islands, and in interior and coastal areas of Baja California, Mexico, including Isla Cedros (SDNHM, UCB Specimens). The larvae feed on green seed in the bladder-like pods of locoweed.

A collection of pods containing larvae of G. vitrana and Everes amyntula (Bdv.) (Lycaenidae) was made from an Astragalus growing on riverine dunes along the Salinas River near King City, Monterey Co. on May 3, 1974 (JAP 74E20). The butterflies emerged within a month, while the tortricids spun tough, papyrus-like cocoons in which prepupal larvae entered diapause. After drying, the lot was stored in the mobile trailer lab on the Berkeley campus. Seven G. vitrana emerged between 28 March and 28 April, 1975. The remaining cocoons were left undisturbed and in the same overwintering conditions except without heat control for 5 weeks in December and January, 1975-76, so were exposed to temperatures of 2° to 4°C on several occasions. Diapause development occurred in 4 individuals  $(2\delta, 29)$ , and moths eclosed between 23 March and 11 May 1976. Similar housing of remaining carryover larvae during the third winter, 1976-77, resulted in 5 more G. vitrana (23, 39) emerging, between 26 February and 17 April, 1977, after 33-35 months in diapause.

Diapause extending to a second or third year has been recorded in several other seed-feeding species of *Grapholita* and the closely related genus *Cydia* (e.g., Dickson, 1949; Hedlin, 1967; Nesin, 1984; Tripp, 1954).

#### COCHYLIDAE

# Cochylis yuccatana (Busck)

This distinctive species is widespread in the southwestern deserts, from Texas (TL: Nuecestown) to southern California and Baja California Norte, Mexico (UCB Specimens). The type series was reared from Yucca baccata; we have found the larvae in flowers of Yucca brevifolia in the Mojave Desert, and Agave shawii in coastal Baja California Norte. There are no records of multiannual diapause, but the species is capable of either completing development without delay or remaining dormant until the following year, which suggests a potential for prolonged diapause exceeding one year.

A single larva taken 5 km W of Palmdale, Los Angeles Co., CA, from *Yucca brevifolia* in late March, 1968, pupated and produced an adult 15 days after collection (JAP 68C62). Several caterpillars feeding on *Agave* near San Telmo, Baja Calif., in mid-March, 1972, did not mature that spring, but two moths eclosed in late April, 1973, after 13 months in diapause (JAP 72C6); while another collection from the same host

near E1 Rosario, Baja Calif., in late March, 1973, produced larvae of both types. Five *C. yuccatana* emerged between 24 April and 8 June, 1973, and one later that summer, and one prepupal larva carried over to complete development in May or June, 1974 (JAP 73C4). Both carryover lots were housed at the Russell insectary.

# PYRALIDAE: CHRYSAUGINAE

# Satole ligniperdalis Dyar

This curious polymorphic and sexually dimorphic species is wide-spread in the southwestern Nearctic, from western Texas to the western edge of the deserts in California (TL = Portal, AZ). Adults have been reared from seed pods of *Chilopsis linearis* (Bignoniaceae) in southern Arizona and southern California (USNM specimens).

A collection of the linear fruits of *Chilopsis* was made by J. T. Doyen on the Kelso Dunes, ca 12 airline km SW Kelso, San Bernardino Co., CA, on July 14, 1974 (JAP 74G9). Ten adults of *S. ligniperdalis* emerged between 18–27 July, and two more later that fall. Although several larvae abandoned the pods by late July and the plant material became badly covered by sooty mould, an apparently healthy larva was revealed by dissecting its cocoon in February, 1975. The lot was therefore placed in a cardboard box and stored in the outdoor cage at Berkeley. Two females emerged in early September, 1975, one on June 25, 1976, and a final one in the fourth season, between October and December, 1977, after 38–40 months in diapause.

Evidently larvae were fully fed at the time of collection and spent diapause as prepupal larvae in cocoons. Because they were held in subdued light and the emergence dates varied by more than two months after late June, it appears photoperiod was not a primary factor influencing diapause development.

## **PYRALIDAE: CRAMBINAE**

# Loxocrambus sp. near mojaviellus Forbes

A somewhat heterogeneous assemblage of specimens from the low deserts of California has been designated as a new species with a manuscript name by A. B. Klots (AMNH). We accumulated large series of this species in a survey of active dune systems of the Colorado and Mojave deserts (Powell, 1978). Included was one specimen that remained unfed, presumably as a prepupal larva in diapause, for 28 months.

The larva was sifted from active dunes south of Rice, Riverside Co., CA, Jan. 30, 1977, by J. T. Doyen and P. A. Rude (JAP 77A19). In early February I opened its sand-covered silken tube to find a large pyralid larva. The larva evidently was fully fed and did not accept plants in the lab. It was retained in a dry container with sand in the mobile trailer

lab (unheated 6 weeks in midwinter) until February, 1978, then in the outdoor cage at Berkeley for one year. Rainfall resulted in wetting the sand once or twice during the 1978–79 winter. After storage in the mobile trailer lab again for four months, a somewhat dwarfed male emerged 1 June, 1979.

#### GEOMETRIDAE

# Eupithecia dichroma - johnstoni group

A single specimen of Eupithecia was reared after spending two winters in diapause, and although the species identification is questionable, the record is noteworthy because prolonged diapause has been recorded for few geometrids. The moth failed to expand its wings fully upon emergence, but it seems to match the description of E. johnstoni McDunnough with only minor differences. The latter species, which was known only from the type male from Inyo County, CA, at the time of McDunnough's revision in 1949, has the whitish ground color on the forewings more contrasting with the red-brown subbasal and subterminal bands than seems to be true of the deformed reared specimen from Modoc County, CA. The male genitalia, particularly the unique aedeagus, confirm a close association with johnstoni and E. rindgei McDunnough, a paler species described from Plumas County, CA. The cornutus is lightly sclerotized basally in the Modoc example, a feature not shown in McDunnough's (1949) illustrations, but otherwise the three species are quite similar in this character.

The geometrid caterpillar was collected incidentally along with larvae of *Pyramidobela quinquecristata* Braun (Ethmidae) and a polyphagous tortricid, *Sparganothis tunicana* (Walsingham), which were webbing and feeding on inflorescences of *Penstemon laetus* spp. *roezlii* (Scrophulariaceae) at Rock Creek, 15 km NE of Adin, Modoc Co., 12 June 1974 (JAP 74F21). Several adults of the *Pyramidobela* and *Sparganothis* were reared within a month; neither of these species diapauses as a prepupal larva or pupa. In late July I discovered a geometrid pupa in the material and placed it in a plastic vial with tissue paper. This was retained in the mobile trailer lab at Berkeley until mid-December, then transferred to the insectary at Russell for 60 days. Examination indicated the pupa to be still alive in August, 1975, and it was again moved to the Russell insectary for overwintering. It was transferred back to Berkeley on 14 March 1976, and the moth emerged 14 days later, after ca 21 months in diapause.

## **SATURNIIDAE**

# Hemileuca electra (Wright)

This fall-flying, diurnal species occurs in southern California, where the larvae feed on *Eriogonum fasciculatum* (Polygonaceae) in spring.

Summer is passed by pupae in diapause. As noted by Comstock & Dammers (1939), in captivity the larvae are susceptible to disease and are difficult to rear.

I collected seven mature larvae at Mission Gorge, San Diego Co., CA, [ca 8 km W of Santee] on *E. fasciculatum*, 19 March 1950. None successfully developed that season, but one pupa held indoors carried over, and a female eclosed 27 November 1951, after 20 months diapause. The capability of emerging following one summer of dormancy or delaying until the succeeding or a later autumn may be characteristic for all species of *Hemileuca*. It has been recorded for *H. maia* (Drury) (Ferguson 1971; W. D. Winter *in litt.*), *H. burnsi* Watson (Comstock and Dammers, 1937), *H. juno* Packard (Comstock & Dammers, 1939), and *H. eglanterina* (Boisduval) (Winter, *in litt.*) and inferred for others by Tuskes (1985).

## Saturnia mendocino Behrens

This diurnal saturniid occurs in the North Coast Ranges and Sierra Nevada of California (Ferguson, 1972), south at least to E1 Dorado Co. (UCB specimen). The larvae have been recorded by several authors to feed on *Arbutus* and *Arctostaphylos* (Ericaceae); Ferguson suggests that *S. mendocino* also feeds on shrubs of other families, apparently based on circumstantial associations for the closely related species, *S. walterorum* Sala & Hogue, in southern California.

David Wagner collected an ovipositing female and egg cluster of S. mendocino on  $Arctostaphylos\ pungens\ var.\ montana\ near\ Alpine\ Lake,$  Marin Co., CA, during a field trip with our immature insects class, on April 13, 1979. The female continued to produce eggs for several days; larvae were reared, May 4 to July 3, 1979, on Arctostaphylos from the U. C. campus (DLW lot L10-14-79). The cocoons were held in an outdoor cage in a plastic bag with damp moss during the 1979-80 winter. Four adults emerged in May, 1980. The remaining pupae were left in a drawer at room temperatures, yet produced two more moths in 1981, none the following year, and one S. mendocino finally emerged in May, 1983, after nearly 4 years in diapause.

Third and fourth year emergence also is recorded in the Palearctic species, *Saturnia pyri* (Schiffermüller), in Maryland (Bryant, 1980).

## **NOTODONTIDAE**

## Pheosia rimosa Packard

I discovered two larvae of this widespread species at Rock Creek, ca 2 km SW of Tom's Place, Mono Co., CA, 26 August 1983, on *Populus trichocarpa* (Salicaceae) (JAP 83H122). The caterpillar, which I mistook for Sphingidae owing to the short caudal horn, was described by Dyar (1891) and others and illustrated in Packard's monograph, but its remarkable crypsis seems not to have been mentioned. The larvae are

peculiar compared to most Notodontidae, being naked, gray, with a greasy or pearly sheen, prominent spiracles and exaggerated intersegmental constrictions. They perch during the day, hanging downward, on the stems of poplar, back of the distal leaves. There they resemble the older stems, which develop rings of enlarged nodal growth that are matched exactly in color by the larvae.

The collection was temporarily housed in a plastic bag and transported in a field ice box during a trip, and one of the larvae pupated loose in the bag by August 31. The larva, pupa and foliage were transferred to a plastic box with sandy soil September 1, but the lot was allowed to become moldy while stored in the mobile trailer lab at Berkeley, and the second larva died. In February, 1984, the material was still damp and the loose pupa on the soil surface was noted to have a thin bloom of mold on its surface and was presumed dead. It was placed in a refrigerator ( $\pm$  4°C) for 5 weeks but did not metamorphose in that season.

The pupa was left in situ on the soil surface and was refrigerated during the 1984–85 winter, from October until February. A large, normally developed female of *P. rimosa*, which is of the pale morph characteristic of populations east of the Sierra Nevada in California, emerged during 16–23 March 1985, after 18 months in diapause. That is, nearly one year later than presumably would be normal for this bivoltine species.

## **NOCTUIDAE**

# Egira crucialis (Grote)

There appear to be few records of prolonged diapause in Noctuidae, although many overwinter as pupae. Thus carryover records of  $Egira\ crucialis$ , for which we do not have accurate emergence dates, seem worthy of recording, to call attention to the potential for extended dormancy in noctuids.

Species of Egira Duponchel (=Xylomyges Gn. and Xylomania Hamp.) are univoltine and fly in early spring, often at quite cold temperatures. In central California they are active from late December to May, the particular flight period varying with the species and elevation. Larvae feed during spring foliation, and pupae in diapause estivate and hibernate until midwinter or spring. We have reared only a few of them, but two  $E.\ crucialis$  remained in diapause beyond the normal spring flight period.

Evidently *Egira crucialis* is a general feeder; we found young larvae on new foliage of *Pseudotsuga menziesii* (Pinaceae), while previous records are from hardwoods. Crumb (1956) listed collections from *Alnus* (Betulaceae) and *Quercus* (Fagaceae) in Washington State, and Prentice (1962) recorded those plant genera as well as *Arbutus* (Ericaceae) and *Salix* (Salicaceae) from Vancouver Island, British Col-

umbia. Our material was taken ca 2 km west of Angwin, Napa Co., CA, 15 May and 1 June, 1979 (DeBenedictis & Powell — JAP 79E62, 79E73). Larvae were reared in polyethylene bags, then transferred to translucent plastic boxes with sterile soil after ca 3 weeks. Pupae in soil-encrusted cells were transferred to the outdoor cage in December and held there until April, 1980. First-year adults should have emerged by this time because in this area E. crucialis flies from mid-February to early April. The collections were not given close surveillance after spring, 1980; they were stored in the mobile trailer lab, without heating for 6 weeks in midwinter. One dead female E. crucialis was found in the 79E73 lot in early April, 1981, and a dead male in 79E62 in June, 1982. The circumstances indicated that both emerged during the 1980–81 winter (i.e., after 18–22 months in diapause), while I was away on sabbatic leave, although the male may have held over an additional year.

## Discussion

Previously unpublished instances of diapause extending one or more years beyond that believed to be normal in the population are reported for 19 species of moths, representing 8 superfamilies. Including these, Table 1 lists taxa for which I have seen records of prolonged diapause in 90 species in 10 superfamilies. This summary is incomplete but reflects the state of knowledge about the taxonomic distribution of the phenomenon in Lepidoptera. The preponderance of records in a few families, Prodoxidae, Saturniidae, Pieridae, and Papilionidae, at least in part indicates rearing efforts, while some taxa such as Geometridae and Noctuidae may be disproportionately underrepresented owing to the failure of lepidopterists to look for viable carryover individuals. It is no coincidence that most of the microlepidoptera listed in Table 1 are Prodoxidae and Ethmiidae, the two families with which I have worked most intensively.

While it would be premature to attempt a detailed summary of the pattern of occurrence of prolonged diapause in Lepidoptera, a few generalizations seem apparent: a) Dormancy persists beyond the normal flight season in prepupal larvae and pupae; it is rare or undetected in adults, eggs, and early instar larvae. b) It has been observed most often in cone- and seed-feeding species that depend upon fruit crops of erratic abundance and in Lepidoptera that live in areas of seasonal drought. c) The ability to carryover appears to be more prevalent among certain butterflies and larger moths than in smaller moths.

The generalization that prolonged diapause is more common in Macrolepidoptera may be a picture painted with too broad a brush; more likely the phenomenon is characteristic of certain taxa, and is rare in others, within most Ditrysian superfamilies. For example, in the Tortricidae, I have seen records of delayed emergence in 8 species, reported

in 17 references by prior researchers, in addition to the one given here. All of these are seed-feeding Eucosmini (1 species) and Grapholitini (7 spp.) (Olethreutinae). Although biologies of a large number of Tortricinae have been studied, apparently prolonged diapause has been reported in none of them. Tortricinae generally and members of the dominant, worldwide tribe Archipini in particular, tend to be species that are indiscriminate in feeding preferences and life cycle pattern, often homodynamic with no fixed dormancy stage. Species that undergo diapause do so as eggs or first instar larvae or in adults; it is very rare in full grown larvae or pupae (Powell, 1964: 17). By contrast, most Olethreutinae are host specific (6% polyphagous vs. 24% in Tortricinae, Powell 1980) with a fixed life cycle, and dormancy commonly occurs in prepupal larvae. Not coincidentally, olethreutines, especially Eucosmini, reach their greatest diversity, while tortricines are depauperate, in desert areas.

On the basis of literature reports and the taxonomic diversity of prolonged diapause among my rather few rearings of desert species, I speculate that most oligophagous Lepidoptera in areas of seasonal drought estivate as prepupal larvae or pupae and that most if not all are capable of producing a facultative second flight and/or carrying over to a subsequent season. Because 2–3 year diapause can occur successfully in tiny moths, such as *Coleophora* in the Turkistan desert (Falkovitch, 1973), we may expect that in groups such as Gelechiidae, which are characteristically diverse in arid and semiarid regions, the capability of prolonged diapause is not rare. For such insects winter temperatures may be important mitigators of diapause development, as in yucca moths, but rainfall has been implicated as critical in some butterflies (e.g., Emmel, 1975:144, and unpubl. *in litt.*; Nakamura & Ae, 1977), as has been documented for various other insects.

Various aspects of diapause and its importance in insect seasonality have been extensively studied, but the physiological mechanisms of prolonged diapause are poorly understood (e.g., Tauber et al., 1986). Presumably particular token stimuli needed to promote the late phases of diapause maintenance and diapause termination are not received. Hence, when thermal or other thresholds are reached that would have resulted in postdiapause development, the diapause maintenance period continues. The degree of individual variation poses interesting, as yet unanswered questions; often some individuals metamorphose, while others exposed to the same stimuli do not. Usually this occurs in environmental conditions that are abnormal, but such variation indicates there are differing genetic factors in diapause potential within colonies, or even among sibs of one egg clutch.

Tauber et al. (1986: 53, 188, 198, 274) have reviewed the role of prolonged diapause in the evolution of seasonality, life histories and speciation. In their discussion there is an assumption which has been made by several authors that extended dormancy regularly occurs in a

certain proportion of the population as an evolutionary bet-hedging tactic. Tauber et al. credit me with recognizing that there are two kinds of prolonged diapause, either a response by whole populations to adverse conditions by carrying over, or a normal, genetically determined occurrence in a certain proportion of the individuals (Powell, 1974). However, I also pointed out that we do not have experimental evidence to demonstrate that there is a fixed polyphenic expression of the genotype, wherein a small number of individuals carry over irrespective of environmental conditions as a kind of buffer against extraordinary climatic extremes. This is still true; in Lepidoptera we do not have data to document that populations of any species express this phenomenon.

In yucca moths (Prodoxus) I have convincing evidence that such genetic predisposition is not the case; under optimum winter environments all or nearly all larvae undergo development, while in adverse conditions all or nearly all maintain diapause (Powell, 1984a, b, 1985). Multiannual emergence patterns such as reported by Carolin (1971) for Coloradia (Saturniidae) appear to represent a fixed polyphenism, but that kind of genetic variability may be manifested only in response to suboptimal climatic situations. Hence, there may not be two discrete classes of prolonged diapause. Rather, populations adapted to erratically variable seasonal and biotic environments may be composed of genetically differing individuals such that none, few, many or all maintain diapause depending upon the degree of fitness to optimum seasonal conditions. With *Prodoxus* it is easy to obtain 100% carryover but almost impossible to promote 100% diapause development under experimental circumstances in the first year. Later, after several years in diapause, individuals will respond to environmental cues that were not sufficient in the first year and proceed through development. This kind of response, rather than a genetically predisposed calendar of events that occurs irrespective of external stimuli, may be producing successive year emergence observed in other insects.

Lepidopterists are urged to record observations such as those given here, particularly the environmental conditions to which dormant stages are subjected, as a necessary step toward more detailed analysis of prolonged diapause.

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# An exceptional case of paternal transmission of the dark form female trait in the tiger swallowtail butterfly, Papilio glaucus (Lepidoptera: Papilionidae)

by

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Abstract. The melanic dark and yellow forms of the tiger swallowtail butterfly,  $Papilio\ glaucus\ glaucus\ L$ ., are believed to be controlled by a locus on the Y (W) chromosome. Since the female is the heterogametic sex (XY) in Lepidoptera, dark females should (and generally do) produce only dark daughters while yellow females produce only yellow daughters. Exceptional broods have been reported in which some yellow females arise from dark, and more rarely some dark females arise from yellow mothers. Scriber et al (1986) have shown that these results (as well as both colors of females arising from either colored mother) can be obtained experimentally by hybridizing and backcrossing with the northern subspecies  $Papilio\ glaucus\ canadensis\ R\ \&\ J$ .

The purpose of this communication is to describe the results of a highly unusual case in which the locus for the dark gene controlling melanism from a dark female *P. glaucus* was transmitted by a male in two separate pairings. This observation has never before been reported and is significant that it suggests that the locus for black color is not necessarily totally lost when it (rarely) dissociates from its normal (Y) chromosome. Since chiasmata at oogenesis in female Lepidoptera are generally believed to be non-existent, crossing-over is believed not to occur in female Lepidoptera. While our results do not permit us to distinguish between a cross-over event and a non-disjunction of the sex chromosome, we nonetheless have observed results of a rare event, especially for Lepidoptera.

#### Introduction:

The melanic dark and yellow forms of the tiger swallowtail butterfly, *Papilio glaucus glaucus* L., are thought to be controlled by a locus on the Y (W) chromosome (Clarke and Sheppard, 1959, 1962). In fact, this locus controlling dark morph expression in female *P. glaucus* is one of

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but a few sex-linked marker genes in butterflies (Robinson, 1971; Soumalainen, 1973; R. Hagen, 1986, and pers. comm.). The female is the heterogametic sex in Lepidoptera, and dark females should (and generally do) produce only dark daughters, and yellow females produce only yellow daughters. Exceptional broods have been reported (Edwards, 1884; Clarke and Sheppard, 1959, 1962; Scriber et al., 1986) in which some yellow females arise from dark, and more rarely some dark females arise from yellow mothers. Scriber et al. (1986) have shown that these results (as well as both colors of females arising from either colored mother) can be obtained experimentally by using hybrids with the northern subspecies Papilio glaucus canadensis R & J. Intermediate colored females with a "peppered" or "sooty" color over the yellow tiger-striped background are also observed in nature (see Edwards, 1884; Clark and Clark, 1951), and have been experimentally produced by hybridization or backcrossing with P. rutulus or P. g. canadensis (Clarke and Willig, 1977; Clarke and Clarke, 1983; Scriber et al, 1986).

In addition to the partial or complete suppression of the Y-linked melanism in female P. glaucus when paired to P. rutulus and P. g. canadensis males (Scriber et al., 1986), it has also been suggested that, if the Y chromosome bearing the locus for the dark gene is occasionally lost during meiosis of dark females, yellow daughters would be produced (Clarke and Sheppard, 1962; Clarke et al., 1976). Scriber et al. (1986) describe such a case in which loss of the locus for dark color in  $\hat{\mathbf{F}}_2$  hybrid females is likely to have occurred. However these authors have also observed cases of yellow  $\mathbf{F}_1$  hybrid daughters of dark mothers which retain the locus for black color. Depending on the male used in subsequent matings, all yellow, all black, or both colors can be obtained from these yellow hybrid or yellow backcross females (Scriber, 1985; Scriber et al., 1986).

Here we describe the results of a highly unusual case in which the locus for the dark gene controlling melanism in female *P. glaucus* seems to have been transmitted by a male to two different handpairings. This situation has never before been reported and is significant in that it suggests that the locus for black color is not necessarily totally lost when it (rarely) dissociates from its normal (Y) chromosome. Since chiasmata at oogenesis in female Lepidoptera are generally believed to be absent, crossing-over is believed not to occur in female Lepidoptera (Haldane, 1922; Robinson, 1971; Clarke and Sheppard, 1973; Soumalainen et al., 1973; Turner and Sheppard, 1975). However a suspected crossover in the supergene controlling female polymorphism in *Papilio memnon* L. has been reported (Clarke and Sheppard, 1977).

Our recent studies of the genetic basis of dark morph expression in *Papilio glaucus* have involved hand-pairings and mass-rearing of thousands of individuals derived from various geographic locations across North America (Scriber and Evans, 1986a). All of these and the

following specimens are maintained in the *Papilio* research collection of J.M.S. at the Department of Entomology at Michigan State University.

#### Results.

A near-normal but slightly melanic or "sooty" (Fig. 1) yellow male adult butterfly was obtained from a normal-appearing dark morph mother (#674) which was field-captured in Adams County, Ohio by M. H. Evans and W. W. Warfield on July 1983. This male eclosed in 1984 and was hand-paired on May 14, 1984 (#1129) to a virgin yellow morph female (P. g. glaucus) which was lab-reared from a yellow morph Ohio female (#631) field-captured on 14 May, 1983. On the following day (May 15, 1984) a second pairing (#1132) using the same male was made to a virgin P. g. canadensis female (which was lab-reared in 1983 from a 25 June, 1983 field-captured yellow female from Barron County, Wisconsin). All subsequent larvae were reared through to pupation under identical controlled environment conditions (16/18 photo/scotophase, corresponding thermoperiod of  $23 \frac{1}{2}$ °C/19  $\frac{1}{2}$ °C). Pupae were weighed and adults were permitted to eclose in cylindrical screen cages.

To our surprise, we observed dark as well as the expected (yellow) females in the progeny of both crosses (Table 1). According to all understanding to date, dark females were not expected to occur in offspring of either of these pairings. We have never before observed dark daughters in the lab-reared offspring of more than 600 different  $P.\ g.\ canadensis$  mothers. While it is possible that  $Papilio\ glaucus$  larvae could be accidentally introduced with foodplant leaves in our laboratory mass rearing procedures at Madison, this is unlikely and careful precautions are continually made to prevent this possibility. We

Table 1. Special case in which an aberrent-colored male mated to two different yellow females resulted in dark female daughters (Madison, WI, 1984).

		Total				Fem eclo	Pupae remaining			
Parentage*	Mating number				Yellow (1984/1985)		Dark (1984/1985)		Dead (n)	Alive (1986)
$OH(Y) \times OH(D)^*$ $Pgc \times OH(D)^*$	1129 1132	69 82	32 40	2 4	9 12	3	16 21	1 0	2	4 2

<sup>\*</sup> Female parent listed first. The OH(D) parent represents an aberrent-colored male (see Fig. 1a and 1b) reared in 1983 from a normal appearing dark morph mother (#674) captured in Adams County, Ohio on 8 July, 1983. This male was mated to a yellow daughter of an Ohio *P. g. glaucus* yellow female #632 on 14 May, 1984 (mating #1129); and to a daughter of *P. g. canadensis* female #614 on 15 May, 1984 (mating #1132).

have not observed any such occurences in the last 5 years with nearly 120,000 ova in our lab. Such errors cannot possibly account for the 38 dark females produced from these two pairings.

#### Discussion.

We interpret the results as evidence of male transmission of the gene controlling black color (which is found on the Y chromosome of the heterogametic female). The sons of pairings 1129 and 1132 were all normal in appearance (i.e. they were not black or dark colored as the female morph can be). Approximately 2/3 of the daughters were dark morph and 1/3 yellow morph, and none of the daughters exhibited partial color or mosaic patterns (e.g. dark with irregular blotches/patches of yellow background showing; see Scriber et al, 1986). This suggests that all cells of dark daughters contain the gene for black color, and favors the idea of non-disjunction or a cross-over of this locus, rather than a particulate cytoplasmic explanation (see Clarke and Sheppard, 1959, 1962).

#### FOLLOWING PAGE CAPTION:

- Fig. 1. Offspring of dark female #674 from Adams Co., Ohio, 1983: a) dorsal and b) ventral of "slightly aberrant" male (wt. 1.1642); c) dorsal and d) ventral of a "normal" sibling (wt. 1.0459). This first (aberrant) is the male parent in crosses 1129 and 1132 (see Table 1), and is our suspected "carrier" of the female melanism locus.
- Fig. 2. F<sub>1</sub> hybrid offspring of pairing #1132 (a virgin daughter of a 1983 Barron Co., Wisconsin *P. g. canadensis* female × the aberrant male, wt. 1.1642, of Fig. 1a & b). a) dorsal and b) ventral of a "slightly aberrant" male (wt. .9386) and c) dorsal and d) ventral of a normal sibling male (wt. .8522).
- Fig. 3. Offspring of an  $F_2$  pairing (#1695; see Table 2) of a dark daughter and a slightly aberrant male (shown in Fig. 2a, 2b) both derived from pairing #1132 (Table 1). a) dorsal and b) ventral of an aberrant male (wt. .9410), and c) dorsal and d) ventral of a normal male sib (wt. 1.0416).
- Fig. 4. Female offspring of a cross between a yellow morph *P. g. glaucus* × the "aberrant" male (cross #1129): a) dorsal and b) ventral of a typical dark morph, (wt. 1.4010) and of a typical yellow morph c) dorsal d) ventral (wt. 1.3700) sibling (see Table 1).
- Fig. 5. Female offspring of  $F_1$  hybrid cross of a P. g.  $canadensis \times$  "aberrant" male P. g. (cross #1132). a) dorsal and b) ventral of a typical dark morph (wt. 0.6964), and c) dorsal and d) ventral of a typical yellow morph (wt. 0.6755) sibling (see Table 1).
- Fig. 6. A wild collected "aberrant" male from Dane County, Wisconsin (collected 10 August 1983).





Under the hypothesis of a non-disjunction as a causal mechanism, we could expect our male to be of the genotype X (XY<sup>D</sup>), where the "Y" represents the Y chromosome carrying the gene for dark color. The P. g. canadensis and yellow morph P. g. glaucus females would both be of the genotype XY, and offspring (1129 and 1132; Table 1) would be expected to be the following: XX and X (XY<sup>D</sup>) males, XY yellow females, and Y (XY<sup>D</sup>) dark females. This explanation would account for the occurrence of both dark and yellow female daughters; however so would the hypothesis of a cross-over event.

In a cross-over of the locus for dark color in this species we would expect the male parent of 1129 and 1132 to be of the genotype  $X^DX$ . When paired to the P. g. canadensis female and the yellow morph P. g. glaucus female (both presumably XY genotype) we would expect the following:  $XX^D$  and XX males, XY yellow females, and  $X^DY$  dark females.

Both the cross-over hypothesis and the non-disjunction hypothesis provide explanations for observed yellow and dark daughters. However, neither explains the observed deviation from an expected 50:50 ratio of female morphs. Similarly, the reason for the melanism being restricted to only (some) daughters and none of the sons of this male carrier (not expressed in himself or his sons) is unresolved for both hypotheses. We did, however, notice a slight "sootiness" or semimelanism in the generally normal tiger-striped yellow background proximally on the dorsal surface of the wings in this original male parent (Fig. 1) and in one of his 44 sons (Fig. 2). We had hoped that this could prove to be a phenotypic marker for the male black locus carriers reflecting the X (XY<sup>D</sup>) or the XX<sup>D</sup> genotype (from either a non-disjunction or a crossover, respectively).

Subsequent pairings with offspring of pairings 1129 and 1132 (Table 1) have yielded poor results. Nonetheless, when the aberrant male son (shown in Fig. 2) was mated to one of his sisters (pairing 1695; Table 2) one of the resulting 5 male  $F_2$  hybrid sons was markedly melanic in the proximal 1/3 of the wings (Fig. 3a, b).

Female offspring resulting from pairings #1129 ( $P.\,g.\,glaucus \times P.\,g.\,glaucus$ ) and #1132 ( $P.\,g.\,canadensis \times P.\,g.\,glaucus$ ) are typical dark or typical yellow in color pattern (Figs. 4 and 5) with one exception, where one daughter is a "dark intermediate". It should be noted that the female progeny of cross 1129 are larger than those of 1132, reflecting the genetic differences in size between  $P.\,g.\,canadensis$  and  $P.\,g.\,glaucus$ . It is also noteworthy that the dark females of cross #1132 represent the only known case of melanism being expressed in  $F_1$  hybrids from a  $P.\,g.\,canadensis$  mother (Fig. 5).

In an attempt to follow up the genetic explanation of our unique results in pairings 1129 and 1132, (Table 1), we hand-paired male, yellow female, and dark female offspring of both crosses. Twenty-one different yellow and dark females from cross 1132 were hand-paired

Table 2. A 1984 F<sub>2</sub> hybrid pairing of a dark female and slight aberrant male (both from pairing 1132; Table 1).

					Fem eclo	Dunge			
Parentage	Mating number				low (1985)		ark (1985)	Pupae alive (1985 October)	
(1132*) <sup>2</sup> * Male with color; date		2	3	1	0	1	1	2	

Table 3. Pairings of a yellow female  $F_1$  hybrid and two of her dark daughters (Madison, WI; 1985).

Parentage	Mating number		Ma eclo (1984)	sed	Yellow (1984)		Da (1984)		Pupae alive (1985 October)
1129(Y) × Pgg* *wild WI male	2343 (see below)	204	_	37	- :	6	-	90	71
2343(DK) × Pgg* *wild OH male	2957	88	_	35	_	0	_	37	16
2343(DK) × Pgg* *wild OH male	2974	81	_	35	_	0	_	36	10

(with copulations of 30 minute durations or more). These pairings resulted in only 8 females which produced eggs, only two of which produced any larvae (#1695 produced 34 larvae, #1542 produced 1 larva). The single most useful cross of these attempts was #1695—an  $F_2$  hybrid of a dark female from  $1132\times$  her aberrent male sibling; see Figs. 2a, 2b. This cross generated both yellow and dark daughters as expected under the crossover/non-disjuction hypotheses (Table 2). Since none of his normal-type siblings (see Figs. 2c, 2d) produced female daughters from fourteen mating attempts, we are unable to evaluate whether this aberrent color in males is indicative of possession of the female melanism gene (i.e. a "carrier" criterion).

Seven different females from cross #1129 were also hand-paired, of which only 3 produced eggs and only one (pairing #2343 in 1985) produced any larvae. This backcross of a yellow morph female (from 1129) to a wild Wisconsin *P. g. glaucus* male resulted in 310 larvae, which produced 204 pupae. Unfortunately, instead of resolving the genetic explanation of the paternal transmission of the melanism

capacity, cross #2343 has become an enigma. This cross involving a yellow mother produced 90 dark daughters, 6 yellow daughters and 37 sons (Table 3). The existence of dark daughters was totally unexpected under our hypotheses of crossover and/or non-disjunction because this female parent (XY) should have produced only yellow daughters. Two subsequent pairings of her dark daughters (#2957 and #2974; also in 1985) to wild male  $P.\ g.\ glaucus$  from Ohio yielded the expected all dark female offspring and an equal sex ratio (Table 3; cf Scriber et al, 1986).

We had hoped that the matings in the 1985 season would clarify our suspected crossover/non-disjunction hypotheses, but this was not the case. At present, we have no explanation for the appearance of dark daughters in pairing 2343 (Table 3). The yellow mother from cross 1129 (Table 2) would presumably have been dark if she possessed the gene for melanism, since any autosomal suppressor in *P. g. canadensis* would not be involved in any pure *P. g. glaucus* lineage (Scriber et al., 1986). However, we are not absolutely certain that the Adams County (Ohio) population is free of *P. g. canadensis* genes from the Appalachian Mountain region (e.g. Ritland and Scriber, 1985; Scriber and Hainze, 1986).

#### Conclusions.

We must emphasize that although we cannot prove a crossover or non-disjunction event, we nonetheless have observed the transmission by a male of the dark morph trait to his daughters (from a mating with a Wisconsin P. g. canadensis yellow female, and from a mating with an Ohio P. g. glaucus yellow female). We do not feel that this phenomenon (appearance of dark daughters from yellow mothers of two different subspecies) is likely to be explained by autosomal melanism suppressor effects from P. g. canadensis introgression. This would require that both the yellow Ohio female and the yellow northern Wisconsin female (the female parents in Table 1) were the result of P. g. canadensis introgression into an ancestrally dark stock. This possibility may not be as farfetched as initially assumed (see Scriber and Evans, 1986a and 1986b). Another remote explanation is that the wild Wisconsin male used in pairing #2343 was simply another independent example of a crossover/non-disjunction, which would also explain dark daughters from a yellow mother presumed to lack the gene for melanism. In this regard it is interesting that partially melanic males (e.g. Fig. 6; and compare Figs. 1, 2, and 3) have been captured from the same population in Wisconsin as the mated male in cross 2343. None have been tested for the dark gene transmission potential however.

Should we be correct in assuming that our results reflect some form of crossover in female Lepidoptera, then there should be special precautions taken by systematists who employ maternal DNA (maternal inheritance of DNA) techniques in evaluating phylogenies, and assume a clear record of the maternal lineage (see Avise and Lansman, 1983)

for further discussion). The adaptive significance of achiasmatic meiosis (and the assumption that this is accompanied by the absence of crossing-over) are not entirely clear, but it has evolved repeatedly in at least 10 major groups of animals (White, 1973). Sexual mosaics, color mosaics, and bilateral gynandromorphs of *Papilio glaucus* may be more common than generally believed, especially near suspected hybrid zones (Clarke and Clarke, 1983; Scriber and Evans, 1986b). Perhaps such chromosomal/developmental abnormalities will provide us with other additional opportunities to evaluate our crossover/non-disjunction hypotheses in the future.

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# The Phenetics and Comparative Biology of *Euphilotes* enoptes (Boisduval) (Lycaenidae) from the San Bernardino Mountains

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Abstract. Euphilotes enoptes larvae in the San Bernardino mountains utilize both perennial and annual Eriogonum species. Many San Bernardino mountain locations have the same Eriogonum species; despite this their utilization as hosts varies amongst populations. Seasonal flight periods which correspond to the initiation of the major host's bloom were not only variable amongst populations, but from year to year. One spring emerging population did not fly during 1984 and 1985 and another had shortened flight periods. Despite differences in hostplants and flight periods, these populations appear to be more closely related in larval setation to each other than to six other described subspecies.

#### Introduction

Populations of *Euphilotes enoptes* (Boisduval) are widely distributed in western North America. They can be found in a variety of habitats from sea level to over 11,000 feet, and from moist cool climates in the Sierra Nevada mountains to the hot dry desert around Palm Springs. The nine described subspecies of this small blue (Miller and Brown, 1981) are often better defined by geographic distribution, flight period, and host plant selection than by adult morphological characters. Distribution of certain subspecies can be quite large as in E. enoptes ancilla (Barnes and McDunnough) covering the seven states, (California, Colorado, Idaho, Montana, Nevada, Oregon, and Wyoming) or extremely small as in E. enoptes smithi (Mattoni) which is found only along the coast of Monterey Co., California (Shields, 1977). The larvae of E. enoptes feed exclusively on blossoms of various Eriogonum species. Most subspecies are known to utilize a single host plant species in a given location and all are believed to be univoltine with the flight season coinciding with the onset of the host flowering period. Various populations fly in every month from March to October.

In southern California two subspecies, *E. enoptes dammersi* (Comstock & Henne) and *E. enoptes mojave* (Watson & Comstock) are recognized. The former flies in late summer and fall in the mountains and foothills of the Colorado and eastern Mojave deserts; its larval hosts are *Eriogonum davidsonii* Greene, *E. elongatum* Benth., *E. wrightii nodosum* (Small) Reveal, and *E. w. wrightii* (Torr.) S. Stokes.

Euphilotes e. mojave flies in the spring in the Mojave Desert and western fringe of the Colorado Desert; its larval hosts are the annuals,  $E.\ pusillum\ Torr.$  and  $E.\ reniforme\ Torr.$  & Frem. Shields (1975) speculated on the basis of similarities in distribution and male genitalia that these subspecies are closely related to each other. The life histories of both subspecies have been published (Comstock & Henne, 1965; Comstock, 1966) but the larval descriptions lack sufficient detail to differentiate them from each other or even other lycaenid species. The present study is an effort to better define the ecological and evolutionary relationships of these 2 taxa and to compare them with other named and unnamed montane populations of  $E.\ enoptes$ .

The San Bernardino Mts. are an extremely complex and interesting geological area. Here the Mojave and Colorado deserts, the coastal chaparral, and the cooler, moister higher elevations of the mountains all meet. Along the northern and northeastern slopes occur spring flying populations of  $E.\ enoptes$ . The northwestern slopes have late summer populations. In the high elevations there are populations that fly in early summer and, depending on rainfall patterns, can be found through mid October. Along the eastern slopes there are populations that fly exclusively in the fall.

# **Materials and Methods**

Studies of E. enoptes in the San Bernardino Mountains entailed numerous field observations at four colony sites (figure 1) to determine seasonal activity, host range, and larval behavior. Doble (DB), el. 6700', (2,000 meters) located at the northeastern end of Baldwin Lake, is an open gently sloped flat of rocky clay soil. The major vegetation consists of short ground cover perennials with scattered Pinus monophylla Torr. & Frem. and Artemisia tridentata Nutt. A second locality (AC) about ten miles (16 km) south-southeast of DB is situated along the steep slope east of Arrastre Creek (AC), el. 7100' (2,200 meters). This site is open with scattered Juniperus occidentalis Hook, P. monophylla, Ceanothus cordulatus Kell, Cercocarpus ledifolius Nutt., and a diverse but sparse community of smaller annuals and perennials; the soil is rocky and porous. A third locality about 12 miles west of DB at Big Pines Flat (BP), el. 6800' (2,100 meters), has uneven terrain with P. monophylla and Pinus ponderosa Dougl. ex P. & C. Lawson forming open stands interspersed with scattered low perennials and annuals. The fourth locality, Mojave River Forks (MR), el. 3100' (950 meters), is 25 miles (40 km) west of DB at the northwestern corner of the San Bernardino Mountains. This site is warmer than the other sites. It is a gently sloped alluvium cut by numerous shallow washes and intermittent creeks; vegetation is diverse, containing elements of Mojave Desert, montane forest, and coastal chaparral communities. Major vegetation includes Juniperus californica Carr., Artemisia tridentata,



Figure 1. Map of the study sites in the San Bernardino Mts, abbreviations as in the Materials and Methods. Line shows 5,000 ft. elevation of mountains.

and Quercus wislizenii A. Dc. with scattered thickets of Adenostoma fasciculatum H. & A., Ceanothus spp., and Cercocarpus betuloides Nutt. ex T. & G. Each of these sites except BP was visited several times during the years 1983 to 1985.

Larvae of *E. enoptes* were also acquired from the following 18 sites (see fig. 2) for comparison of setal characters:

(**BG**) Bob's Gap, N. base San Gabriel Mts., Los Angeles Co., Ca., el. 4000' (1200 meters), 22. V. 83., on *E. pusillum* GRB; (*E. e. mojave*)

(CC) Chino Canyon, San Jacinto Mountains, Riverside Co., Ca., el. 2600' (800 meters), 27. IX. 83., on *E. davidsonii* and *E. w. nodosum*, GRB & GFP; (Type locality for *E. e. dammersi*)

(CS) Upper Centennial Spring, Coso Range, Inyo Co., el 6100' (1900 meters), 1. VIII. 83., on *Eriogonum nudum* Dougl. ex Benth., J. F. Emmel; (subspecies undefined)

(EP) E1 Paso Mountains, vic. Last Chance Canyon, Kern Co. Ca., el. 2500' (760 meters), 19. V. 83., on *E. nudum*, GRB & GFP; (undefined subspecies near *E. e. mojave*)

(LH) Landels Hill Big Creek Reserve, Monterey Co., Ca., el. < 100' (30 meters), 17, VIII. 84., on  $Eriogonum\ parvifolium\ Sm.$  in Reese, GFP; ( $E.\ e.\ smithi$ )

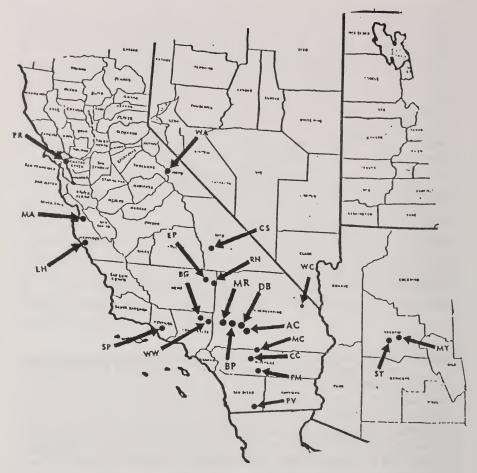


Figure 2. Map of the collection sites; abbreviations as in the Materials and Methods.

(MA) Marina, Monterey Co., Ca., el. < 100' (30 meters), 22. VII. 83. on  $Eriogonum\ latifolium\ Sm.$  in Reese, GRB; (E. e. smithi)

(MCA) Big Morongo Canyon, Riverside and San Bernardino Cos., Ca., el. ca 2000" (600 meters), 17. IV. 84., on *E. pusillum*, GFP; (*E. e. mojave*)

(MCS) same data as above except 15. IX. 84., on *Eriogonum elongatum Benth.*, GPP; (E. e. dammersi)

(MY) Mayer, Yavapai Co., AZ., el. 4500' (1400 meters), 15. X. 82., on E. w. wrightii, GRB; (E. e. dammersi)

(PM) Pyramid Mountain, San Jacinto Mountains, Riverside Co., Ca., el. 6000' (1800 meters), 17. VI. 82., 6 VI. 83., 1. VII. 83., 26. V. 84., on *E. davidsonii*, GRB & GFP; (subspecies undefined)

(**PR**) Point Richmond, Contra Costa Co., Ca., el. < 100' (30 meters), 23. VII. 83., on *Eriogonum nudum auriculatum* (Benth.) Tracy ex Jeps., GRB; (*E. e. bayensis*)

(PV) 28 mi. E. of Pine Valley on HWy. 8, San Diego Co., Ca., el. 3500' (1100 meters), 26. VII. 84., on  $E.\ elongatum$ , GRB; ( $E.\ e.\ dammersi$ ) (RN) Randsburg, Kern Co., Ca., el. 3500' (1100 meters), 19. V. 83., on  $E.\ pusillum$ , GRB & GFP; ( $E.\ e.\ mojave$ )

(SP) Santa Paula, Ventura Co., Ca., el. 1000' (300 meters), 20. VI. 84.,

on E. parvifolium, GFP; (E. e. tildeni)

(ST) Stanton, Yavapai Co., Az., el. 3500' (1100 meters), 15. X. 82., on E. w. wrightii, GRB; (E. e. dammersi)

(WA) Warren Canyon, near Tioga Pass, Mono Co., Ca., el. 9000' (2700 meters), 17. VII. 83., on *E. nudum*, GRB & GFP; (*E. e. enoptes*)

(WC) Wildhorse Canyon, Mid Hills, eastern Mojave Desert, San Bernardino Co., CA., el. 4000' (1200 meters), 2. X. 82., on  $E.\ w.\ wrightii$ , GRB & GFP; ( $E.\ e.\ dammersi$ )

(**WW**) Wrightwood, 1 mi. W., Los Angeles Co., Ca., el. 6000' (1800 meters), 7. IX. 82. and 13. VIII. 83., on *E. nudum saxicola* (Heller) S. Stokes, GRB & GFP; (Shields, 1977, places populations from this area in the nominate subspecies but they may be closer to *E. e. tildeni*)

Larvae were obtained by beating host plant inflorescences, searching for floral shelters, or by rearing from ova. Ova and larvae were often found with other lycaenid species including *Celastrina argiolus* (Linnaeus), *Hemiargus ceraunus gyas* (W. H. Edwards), *Icaricia acmon* (Westwood & Hewitson), *Icaricia neurona* (Skinner), and *Strymon melinus* Hubner. Ova of *E. enoptes* were easily distinguished by their poorly defined chorionic ridges, and larvae were separated by setal outlines. Although color can be variable, larvae of *E. enoptes* are usually yellow or white (never green) with pink or red chevron markings while larvae of the other species are often green. Samples of larvae from all localities were injected with Kahle's fluid, fixed in hot water, and stored in 80% ethanol.

Often larvae were reared on host plants from their collection sites; occasionally, other hosts were substituted. Since E enoptes larvae are cannibalistic they were reared individually in screened vials with flower stalks placed in water to maintain freshness; flowers were frequently changed to avoid mold. Most larvae were permitted to pupate in soil or the rearing container. Pupae were kept under a variety of conditions, as shown in Table 1. Eclosion dates were recorded.

As with most Lycaenids, mature (fourth instar) larvae (Langston and Comstock (1966) and Arnold (1983) state that *E. enoptes bayensis* and *E. e. smithi* respectively have 5 instars, yet in hundreds of rearings of various *E. enoptes* populations we have found only four instars of *E. enoptes*) are covered with short secondary setae and possess a variable number of more prominent (longer and erect) setae grouped in locations where primary setae should occur (sensu Hinton, 1946) (Fig. 3). These locations are dorsal (just lateral to the midline), subdorsal (slightly dorsal to the line of spiracles), and lateral (along the lateral fold). Also, on the prothorax, a few prominent setae occur on the shield

Table 1. Pupae initially kept at 27–35°c were refrigerated (5°c) for at least two months ending in December; afterwards they were kept at 22–27°c. Pupae initially kept at 22–27°c were refrigerated from Dec. 22, 1983 to April 3, 1984 and returned to 22–27°c. Those pupae not refrigerated first year were refrigerated with other pupae their second year for 2–3 months. Those pupae not refrigerated were subjected to moderated daily fluctuations in temperature. The number of pupae from each site is shown in parenthesis.

Pupae kept at 27 – 35°c	Pupae kept at 22–27°c	Pupae not refrigerated first year	Pupae not refrigerated
AC (4)	BG (5)	MY (1)	BP (5)
EP (7)	BP (9)	ST (1)	MR (3)
LH (25)	CC (3)	WC (3)	DB (54)
McA (15)	DB (8)		SP (3)
McS (65)	EP (8)		MA (1)
PM (7)	MR (5)		
PV (2)	PM (1)		
	PR (9)		
	PV (6)		
	WA (2)		
	WW (3)		

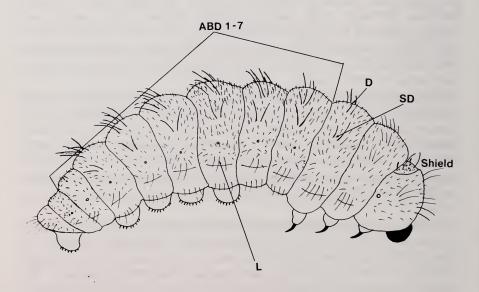


Figure 3. Diagram of an *E. enoptes mojave* larva showing the positions of the setae counted for the 11 characters. Those positions are (D) Dorsal, (SD) Subdorsal, (L) Lateral, (ABD 1-7) Abdominal Segments 1 to 7, and (Shield) Prothoracic Shield.

and many more are located in front of the shield and ventrolateral to the shield in poorly defined groups. Elsewhere, prominent setae occur in specified locations and are most abundant on the mesothorax. No apparent difference in number of prominent setae was found among abdominal segments 1-6 but an increase in number of lateral prominent setae was often noted on the remaining segments. No prominent dorsal setae occur on the seventh abdominal segment in the region of Newcomer's organ (honey gland); also none occur on the more posterior segments.

Both the number and size of prominent setae vary. For comparative purposes the total prominent setae in each location (both sides of the larva) were summed for each segment. Prominent setae were given a value of one if they were at least twice (>0.2 mm) as long as surrounding secondary setae and one-half if they were 1.5-2 times (0.15-0.2 mm) as long as the secondary setae.

Prominent setae in eleven locations were quantified and subjected to statistical analysis using Duncan's Multiple Range Test. These locations were: (1) prothoracic shield, (2) dorsally on the mesothorax, (3) dorsally on the metathorax, (4) dorsally on abdominal segments 1–6, (5) subdorsally on the mesothorax, (6) subdorsally on the metathorax, (7) subdorsally on abdominal segments 1–6, (8) laterally on the mesothorax, (9) laterally on the metathorax, (10) laterally on abdominal segments 1–6, and (11) laterally on abdominal segment 7. Prominent subdorsal setae on abdominal segment 7 and prominent lateral setae on abdominal segments 8–10 may offer characters for statistical analysis but were not included.

A variable number of larvae were used to represent each population; the minimum number was 6 the maximum 30. Consecutive generations of larvae were sampled at DB in June (DB1) and July (DB2) 1983. Samples were taken from MR in September 1982 (MR1) and October 1983 (MR2). These populations were compared statistically to ascertain the stability of mean character states. For the populations PM and WW, larvae from consecutive generations were pooled.

Tables 2-5 present the results of statistical analysis. Populations are listed according to specified abbreviations followed by the number of larvae (n), character mean, standard error, and results of Duncan's Test at the 1% error level.

#### Results

Larval setation analysis separates the  $E.\ enoptes$  populations studied herein into 4 basic groups. The populations of  $E.\ e.\ mojave$  (MCA, BG, RN) have the largest mean number of prominent setae. The number of prominent setae for these populations is significantly higher than for all other populations in dorsal, subdorsal, and lateral positions. With population EP they also have a significantly higher mean number of prominent setae on the prothoracic shield.

Population EP ranks next in mean number of prominent setae in the same locations. It differs significantly from all other populations in prominent setae dorsally on all segments (Table 2) and laterally on abdominal segments 1–7 (Tables 3 and 5). EP and PM together differ significantly in prominent subdorsal setae on the metathorax (Table 2).

Populations CS, PM, and WA often rank together with means higher than all other populations except those above. They are not significantly different from each other in mean number of prominent dorsal setae on all segments and prominent subdorsal setae on abdominal segments 1–6. PM and WA differ significantly from other populations in prominent lateral setae on abdominal segments 1–6; they differ significantly from each other, but not from CS, in prominent subdorsal setae on the mesothorax and prominent lateral setae on the metathorax. PM and CS differ significantly from each other but not from WA in lateral prominent setae on abdominal segment seven.

There is little overall difference in mean number of prominent setae among the populations AC, DB1, DB2, BP, CC, LH, MA, MR1, MR2, MY, PR, PV, SP, ST, WC, and WW. For all setal characters they either do not differ significantly from each other or form a series of overlapping nonsignificant subsets. Populations DB1 and DB2, which represent consecutive generations in June and July, respectively, differ slightly, but not significantly, for all means, except subdorsal setae on abdominal segments 1–6; these are identical. Populations MR1 and MR2, which represent consecutive generations at MR in 1982 and 1983, respectively, differ slightly but not significantly for all means except prominent dorsal setae on the metathorax and dorsal and subdorsal setae on abdominal segments 1–6; these are identical.

Character means for the San Bernardino Mountains populations, (AC, DB1, DB2, BP, MR1, MR2), generally do not differ significantly. However, the mean number of prominent setae on the prothoracic shield is significantly higher for AC than for DB2 and MR2. Also, DB1 differs significantly from MR1 and BP in mean number of prominent dorsal setae on the mesothorax; it also differs significantly from MR1 in mean number of prominent lateral setae on the metathorax and from both MR1 and MR2 in mean number of prominent lateral setae on abdominal segment seven.

According to field observations (Table 6) there are at least three separable populations of E. enoptes in the San Bernardino Mts. The one at AC is single brooded and can be found only in the spring. Another population (BP and MR) occurs as adults during late summer and early fall. At DB E. enoptes appears in early spring, but can be found, depending on rainfall, into early fall overlapping the flight periods of the two other populations. The rainfall patterns also affected AC and MR over the three years. The spring of 1983 was wet, whereas both 1984 and 1985 were seasonably dry. This may account for adults

emerging up to 2 weeks earlier at DB and MR, and both larvae and adults at AC absent during 1984 and 1985.

Weekly visits to MR during 1982 and 1983 revealed no *E. enoptes* adults or larvae prior to August 21 except three larvae on *E. pusillum* (29. V. 1982) which had similar setation to *E. e. mojave* larvae from BG, MCA, and RN. Although *E. elongatum* and *E. wrightii trachygonum* normally do not bloom until August, *E. davidsonii* is abundant at MR and blooms from spring to summer. However, the only lycaenid larvae found on *E. davidsonii* at MR were *I. acmon*.

The eclosion dates for pupae from the four San Bernardino Mountain sites correspond to field observations. All pupae from DB failed to diapause. Of four AC pupae, initially kept at  $27-35^{\circ}\mathrm{C}$ , one failed to diapause, while the other 3 eclosed within four weeks after removal from refrigeration in January 1984. Three of five pupae from BP did not diapause at  $27-35^{\circ}\mathrm{C}$ . The remainder were kept at unheated Riverside temperatures from December 1983 until they eclosed in July and August 1984. Nine other BP pupae were kept at  $22-27^{\circ}\mathrm{C}$ , and refrigerated from December 28, 1983 to April 3, 1984. They eclosed from May 30, 1984 to July 27, 1984. Five MR pupae were refrigerated and incubated with those from BP, and eclosed July 9, 1984 to Sept. 2, 1984. Another three MR pupae were not refrigerated but kept at  $27^{\circ}\mathrm{C}$ , as with those from BP, and eclosed mid July to mid August 1984.

All three pupae from MY, one from ST, and five from WC eclosed during September and October 1983. In 1984 (after refrigeration treatment) two more from WC eclosed in July and August; one pupa each from ST and WC still remained in diapause.

A variable number of pupae from most locations eclosed within four weeks when initially kept at  $27-35^{\circ}\mathrm{C}$ . These include those from the San Bernardino Mountains, as noted above, DB (50), EP (2), LH (21), MCA (3), MCS (4), PM (1), SP (3), WA (3), and WC (2). Of the pupae initially kept at  $22-27^{\circ}\mathrm{C}$  only those from PV (6), WA (2), and DB (8), failed to diapause.

Many pupae eclosed within 4-5 weeks after removal from refrigeration in December. These include EP (5), MCA (12), and PM (5); one pupa from PM did not eclose in the winter of 1983 but, after a second season including refrigeration again, eclosed in January 1984.

Larvae of *E. enoptes* were found on five species of *Eriogonum* in the San Bernardino Mountains. *Eriogonum davidsonii* is an annual which begins to bloom in spring and may continue into summer and fall, depending on soil moisture. It is the only apparent host of *E. enoptes* at AC and may be the preferred host at BP, since about twice as many larvae were found on it as on *E. wrightii subscaposum*. This plant is absent from DB. At MR it blooms primarily in spring. *Eriogonum kennedyi*, which occurs in a few isolated sites in the San Bernardino Mountains, begins to bloom in May or June; at DB it bloomed during May and June to September during 1983. In 1984 at DB it bloomed

Table 2. The mean total prominent dorsal setae on the mesothorax, metathorax, and abdominal segments 1 through 6; means followed by the same letter are not significantly different at the 1% level.

		meso-			meta-			A		
		tnorax			thorax			1-6		
Locality	n	mean	S. E.	1%	mean	S. E.	1%	mean	S. E.	1%
MCA	23	8.04	0.54	А	4. 41	0.53	A	19. 37	1.37	A
BG	17	7.18	0.51	AB	3.88	0.44	A	19.76	1.20	А
SN	19	6.58	0.43	B	4.21	0.38	A	21.11	1.41	A
EP	18	4.72	0.44	С	1.78	0.35	В	10.33	1.59	B
₩A	12	3.42	0.29	D	0.00	0.00	ε	0.00	0.00	C
PM:	17	3.24	0.39	D	0.42	0.19	С	2.44	0.88	С
DS .	14	3. 07	0.21	D	0.00	0.00	C	0.00	0.00	С
BL:	23	1.08	0.23	EF	0.09	0.06	ε	0.13	0.13	С
SP	6	1.17	0.48	EF	0.00	0.00	С	0.00	0.00	С
Wh.	18	1.08	0.27	EF	0.00	0.00	ε	0.00	0.00	C
PR	26	0.98	0.20	EF	0.00	0.00	С	0.00	0.00	0
BL2	17	0.91	0.26	EF	0.00	0.00	С	0.00	0.00	С
#R2	22	0.57	0.21	EF	0.00	0.00	С	0.00	0.00	С
AC	8	0.21	0.21	· F	0.00	0.00	С	0.00	0.00	C
LH	30	0.37	0.13	F	0.00	0.00	С	0.00	0.00	С
23	7	0.29	0.29	F	0.00	0.00	С	0.00	0.00	ε
BPF	14	0.28	0.15	F	0.00	0.00	C	0.00	0.00	С
MY	9	0.22	0.22	F	0.00	0.00	С	0.11	0.11	C
MCS	27	0.20	0.10	F	0.00	0.00	С	0.00	0.00	C
ST	13	0.19	0.05	F	0.00	0.00	C	0.05	0.03	C
WC	21	0.05	0.03	F	0.00	0.00	C	0.00	0.00	£
PV	15	0.03	0.03	F	0.00	0.00	C	0.00	0.00	C
MR1	17	0.03	0.03	F	0.00	0.00	C	0.00	0.00	C
MA	10	0.00	0.00	F	0.00	0.00	С	0.00	0.00	C

Table 3. The mean total prominent sub-dorsal setae on the mesothorax, metathorax, and abdominal segments 1 through 6; means followed by the same letter are not significantly different at the 1% level.

		meso-			meta-			abd.		
		thorax			thorax			seg.		
Locality	n	mean	S.E.	1%	mean	S.E.	1%	1-6	S. E.	1%
MCA	23	7.80	0.64	А	4. 28	0.28	A	12.80	1.69	А
RN	19	7.21	0.41	A	4.74	0.30	A	10.63	1.39	A
86	17	6.7€	0.65	A	4.41	0.41	A	11.47	1.29	A
EP	18	4.67	0.29	В	2.22	0.11	В	1.33	0.62	B
PM	17	4.24	0.32	B	1.88	0.30	B	1.06	0.69	В
CS	14	3.50	0.39	BC	0.75	0.20	С	0.00	0.00	В
₩A	12	2.50	0.15	CD	0.08	0.06	С	0.00	0.00	В
DB1	23	2.48	0.24	CD	0.43	0.15	С	0.00	0.00	В
DB2	17	2.29	0.28	CDE	0.32	0.18	С	0.00	0.00	В
AC	8	2.13	0.30	CDE	0.56	0.30	С	0.00	0.00	В
MR2	22	1.80	0.26	DE	0.09	0.09	С	0.00	0.00	В
CC	7	1.79	0.46	DE	0.00	0.00	С	0.00	0.00	B
MΥ	9	1.78	0.32	DE	0.00	0.00	C	0.00	0.00	В
PV	15	1.77	0.19	DE	0.07	0.07	С	0.00	0.00	B
ST	13	1.69	0.29	DE	0.00	0.00	C	0.00	0.00	В
MR1	17	1.56	0.31	DE	0.00	0.00	0	0.12	0.07	B
LH	30	1.52	0.20	DE	0.00	0.00	С	0.00	0.00	B
MCS	27	1.44	0.21	DE	0.00	0.00	С	0.00	0.00	B
PR	26	1.44	0.14	DE	0.00	0.00	С	0.00	0.00	B
WH	18	1.31	0.19	DE	0.03	0.03	С	0.00	0.00	B
MA	10	1.20	0.29	DE	0.00	0.00	С	0.00	0.00	В
MC	21	1.17	0.19	DE	0.00	0.00	С	0.02	0.02	B
SP	6	1.17	0.65	DE	0.00	0.00	С	0.00	0.00	B
BP	14	0.89	0.27	E	0.00	0.00	С	0.00	0.00	B

Table 4. The mean total prominent lateral setae on the mesothorax, metathorax, and abdominal segments 1 through 6; means followed by the same letter are not significantly different at the 1% level.

		meso- thorax			meta- thorax			abd. seg.		•
Locality	n	mean	S. E.	1%	mean	S. E.	1%	1-6	5. E.	1%
WA	12	10.83	0.37	A	6.75	0.37	AB	12.29	1.26	С
LH	30	10.05	0.42	AB	3.88	0.42	CDEF	0.95	0.32	D
MCA	23	9. 91	0.64	AB	8. 43	0.54	A	43.28	2.95	Α
CS	14	9.64	0.39	ABC	5.14	0.31	BC	5.36	1.38	1
ΞP	18	9.33	0.63	ABCD	6.78	0.45	AB	30.06	2.65	В
RN	19	9.26	0.21	ABCD	7.47	0.39	A	46,53	1.76	Α
SP	6	9.00	0.26	ABCDE	4.25	0.60	CDE	0.00	0.00	1
BG	17	8.76	0.28	BCDE	7.35	0.23	A	43.24	1.49	Α
MA	10	8.50	0.54	BCDE	4.10	0.55	CDE	0.10	0.10	I
PR	26	8.04	0.30	BCDEF	4.58	0.41	CD	0.73	0.38	1
BP	14	7.79	0.58	CDEF	3.00	0.50	DEFEH	1.46	0.54	1
WW	18	7.50	0.44	DEFG	3.06	0.45	DEFG	0.64	0.30	I
PM	17	7.00	0.33	EF6	5.00	0.33	С	16.71	1.69	C
DB2	17	7.00	0.23	EFG	2.41	0.38	EF6HI	0.88	0.46	ī
DB1	23	6.96	0.29	EF6	3.07	0.27	DEFG	2.17	0.79	1
MR2	22	6.45	0.42	F6H	1.18	0.42	HIJ	0.05	0.05	ľ
MR1	17	6. 18	0.54	FGH	2.12	0.51	F6HIJ	0.00	0.00	1
AC	8	6.13	0.35	FGH	2.13	0.40	FGHIJ	0.63	0.30	ī
MY	9	6.00	0.87	F6H	0.67	0.47	IJ	0.00	0.00	1
20	7	5.71	0.57	6H	0.29	0.18	J	0.00	0.00	Ī
PV	15	5.67	0.31	6H	0.90	0.32	1 <b>J</b>	0.07	0.07	1
MCS	27	5.65	0.26	GH	1.69	0.26	GHIJ	0.00	0.00	Ī
WC	21	4.86	0.48	H	0. 43	0.16	J	0.00	0.00	1
ST	13	4.54	0.49	н	0.69	0.26	IJ	0.00	0.00	I

Table 5. The mean total prominent setae on the prothoracic shield and laterally on abdominal segment 7; means followed by the same letter are not significantly different at the 1% level.

		setae			setae		
	O	n shield			abd.seg.7		
Locality	n	mean	5. E.	1%	mean	5. E.	1%
RN	19	3.47	0.19	А	7.58	0.50	Α
BG	17	3.12	0.23	AB	7.41	0.37	A
EP	18	2.72	0.24	AB	5.33	0.54	В
MCA	23	2.48	0.15	В	7.98	0.34	A
PM	17	1.71	0.24	C	3.47	0.42	С
WA	12	1.67	0.22	C	2.58	0.19	CD
WW	18	1.39	0.20	CD	0.67	0.23	EF6
AC	8	1.38	0.38	CD	0.63	0.32	FG
PR	26	1.23	0.17	CDE	1.06	0.17	EFG
CS CS	14	0.93	0.22	CDEF	1.86	0.23	DE
DB1	23	0.91	0.21	CDEF	1.43	0.18	EF
MA	10	0.70	0.21	DEFG	0.50	0.27	FG
MR1	17	0.68	0.21	DEFG	0.12	0.12	G
Bb	14	0.57	0.20	DEFG	0.46	0.19	FG
LH	30	0.53	0.14	EF6	0. 97	0.19	EF6
DB2	23	0.53	0.17	EFG	1.06	0.22	EFG
SP	6	0.33	0.33	F6	0.33	0.21	FG
WC	21	0.24	0.10	F6	0.00	0.00	G
MR2	22	0.18	0.08	FG	0.09	0.09	6
CC	7	0.14	0.14	FB	0.29	0.18	FG
MCS	27	0.11	0.06	FG	0.19	0.08	6
PV	15	0.07	0.07	6	0.17	0.09	G
ST	13	0.00	0.00	6	0.00	0.00	G
MY	9	0.00	0.00	G	0.11	0.11	G

Table 6. The weeks of each month on which L — larvae or A — adults were observed at the 4 different San Bernardino Mt. sites.

		ok	oser	ved	at	the	4 different San Bernardino Mt. sites.													
		M	ΑY		JU	JUNE			JUL	Υ		AUGUST			Γ	SEPTEMBER			R	ост.
		3	4	1	2	3	4	1	2	3	4	1	2	3	4	1	2	3	4	1
AC:	1983					AA	L	L	L											
BP:	1983																L			
	1985																L			
DB:	1983			AL		Α					AL	AL					Α			
	1984		AL		AL															
	1985	Α		AL																
MR:	1983													Α		Α	AL	AL	L	L
	1984														L	L				
	1985													Α	Α	L				

during May and June and again in September after summer rains. *Eriogonum wrightii subscaposum*, which is common and widespread above 5000' in the San Bernardino Mountains, blooms from August to October. This plant is utilized by *E. enoptes* at BP and DB. *Eriogonum wrightii trachygonum*, which is common mostly below 5000', also blooms from August to October. This plant is utilized by *E. enoptes* at MR. *Eriogonum elongatum*, a common species below 5000', especially along the southern slopes of the San Bernardino Mountains, blooms primarily from August to October. It is the major host of *E. enoptes* at MR.

The presence of the aforementioned hosts does not always correspond to the presence of *E. enoptes*. At MR no *E. enoptes* larvae were found on E. davidsonii; nor were any found on E. wrightii at AC. Both of these plants are common at many sites in the San Bernardino Mountains where E. enoptes has not been found. Eriogonum elongatum and E. nudum, which is utilized by E. enoptes in the adjacent San Gabriel Mountains, are widespread and abundant at many sites along the southern slopes of the San Bernardino Mountains yet no populations of E. enoptes are known to utilize them there. Eriogonum umbellatum Torr., another common species above 6000', is a preferred host for some populations of both *Euphilotes battoides* (Behr) and *E. enoptes*, but is utilized by neither in the San Bernardino Mountains. In fact, E. enoptes larvae from MR die when fed the local *E. umbellatum munzii* (Reveal) as do larvae of E. battoides glaucon (Edwards) (J. F. Emmel, personal communication), which utilizes another subspecies of E. umbellatum in the Sierra Nevada.

Observations of larval behavior were noted for several populations of  $E.\ enoptes$ . In the field, larvae from LH, MR, SP, WW, AC, and PM, often tie together dry and partially consumed flowers to create loose shelters within the host inflorescence. At Morongo Canyon (MCS) mostly first and second instar larvae, rather than later instars, as expected, were found on the host  $E.\ elongatum$  from September 15 to November 24, 1984. Under laboratory conditions, these larvae matured to third and fourth instars. The larvae fed nocturnally and remained concealed at the base of host plants by day; they made no floral shelters. Field evidence (the lack of mature larvae on blossoms) suggests that larvae from CC and PV may have a similar behavior.

## Discussion

Adult eclosion has two determining factors: conditions which terminate diapause, and thermal summation for subsequent development. Pupae which break diapause simultaneously may eclose at different times in the field due to different temperature regimes (in their environments). Euphilotes enoptes pupae from some populations break diapause in response to warming after cold treatment, while others may break diapause in response to other conditions, perhaps independent of cold treatment. When reared under the same conditions, early-flying populations eclose soon after the end of refrigeration, independent of the time of year, while late-flying populations do not eclose until several weeks or months later. Both types of diapause occur in the San Bernardino mountains and one population is facultatively multivoltine.

A high temperature regime  $(27-35^{\circ}\text{C})$  during development is more conducive to breaking diapause (or inhibiting its induction) in E. enoptes than is a lower temperature regime  $(22-27^{\circ}\text{C})$ . This has been shown in other insects as well (Chapman, 1971). Other E. enoptes populations (PV and WA), in addition to the Doble population, appear to be at least bivoltine, as indicated by their pupae failing to diapause when kept at  $22-27^{\circ}\text{C}$ .

Conditions which induce diapause in the multivoltine DB population are not known, but probably are related to host plant condition and/or moisture stress. Some  $E.\ enoptes$  pupae can also diapause for more than one year. Termination of diapause in these populations may be affected by rainfall patterns, temperature, and/or photoperiod.

Various populations of E. enoptes utilize several species of Eriogonum in the subgenera Eucycla and Ganysma (Reveal, 1969). In the San Bernardino Mountains E. enoptes utilizes at least four Eriogonum species belonging to both subgenera and often more than one in a given locality. However, not all available hosts are utilized nor are the acceptable hosts utilized wherever they occur. Thus, the distribution of E. enoptes in this area is largely independent of availability of hosts.

Euphilotes e. mojave may have the most restricted diet of the E.

enoptes subspecies. So far it has been found only on *E. pusillum* and *E. reniforme* even at sites where other hosts occur, as at BG where *E. davidsonii* grows along side *E. pusillum*. Larvae of *E. e. mojave* from MCA collected on *E. pusillum*, which would switch to *E. reniforme* in the lab would not feed on *E. davidsonii* or *E. nudum*. Yet larvae of *E. enoptes* from MR2 collected on *E. elongatum* easily switched to *E. davidsonii*, *E. pusillum* and *E. microthecum*.

First and second instar E. enoptes remain within host plant inflorescences. Third and fourth instars, from some populations, often create shelters by tying blossoms together with silk, where they remain until mature or until food is depleted. Older larvae of E. e. dammersi at Morongo Canyon do not make floral shelters but probably conceal themselves at the plant base by day and feed on blossoms nocturnally, or crepuscularly. Similar behavior may also occur in some other populations of E. e. dammersi.

Setation patterns of mature larvae vary among populations of E. enoptes. These patterns are relatively constant from generation to generation and offer reliable characters for comparing different populations. Many populations (E. e. bayensis, E. e. dammersi, E. e. enoptes, E. e. enoptes larvae have few prominent setae dorsally and dorso-laterally, but a relatively large number laterally on all segments. Larvae of E. e. enoptes have far more prominent setae than the other subspecies in nearly all body regions. This permits them to be readily distinguished from the others.

Larvae of populations of E. enoptes in the San Bernardino Mountains more closely resemble setal patterns of E. e. dammersi than E. e. mojave, both of which occur nearby. At sites where both E. e. mojave and another subspecies of E. enoptes occur, as at Mojave River Forks and Morongo Canyon, there is no apparent dilution of larval characters in either. Therefore, it seems unlikely that any gene mixing occurs. Of course, in both cases their flight seasons are widely separate.

The similarity in larval setation of the San Bernardino Mountain populations suggests that these are closely related. San Bernardino Mountains populations of  $E.\ enoptes$  are more-or-less intermediate in setal characters between the  $E.\ e.\ dammersi$  populations to the east and populations of  $E.\ e.\ bayensis,\ E.\ e.\ smithi,\ and\ E.\ e.\ tildeni$  to the west.

#### **General Conclusions**

Larval hostplant and setation characters can be utilized to consistently separate certain populations of subspecies of *E. enoptes* from others. Among the other subspecies (at least *E. e. dammersi*, *E. e. smithi*, *E. e. tildeni*, and the San Bernardino Mountains populations) host plant specificity and seasonal flight period are variable from location to

location. The plasticity of these characters may render them unreliable as indicators of subspecific relationships.

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# A New Genus and Species from the Southwestern United States (Noctuidae: Acontiinae)

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Abstract. The species albiciliata Smith (1903) is removed from the genus Cobubatha Walker 1863, and made the type of a new genus, Allerastria. The genitalia of albiciliata are described, apparently for the first time. Three new taxa are described in the new genus, two subspecies of albiciliata (paula, from the San Joaquin Valley, California, and chacoensis, from the Chaco Canyon National Monument, New Mexico) and a new species (annae from southern california). All species and subspecies are figured and diagnosed.

### Introduction

In 1977 I took a long series of *Cobubatha albiciliata* (Smith) at the western mouth of Titus Canyon, on the valley floor of Death Valley National Monument. Mixed with this series was a short series of moths that could not be assigned to *albiciliata* and is described as new. With the borrowing of additional material and the investigation of the other species of *Cobubatha* a number of characteristics were found that separated *albiciliata* and the new species from *Cobubatha*.

From the time *albiciliata* was described in 1903 by Smith, it has had uncertain placement. Smith (1903) stated "the species is not really an *Yrias*, but it resembles that genus in general form and may remain here until further material makes a better reference possible." Barnes and McDunnough (1912) in their description of the synonym *bifasciata* were not certain of the generic assignment when they placed "the species for the present in *Eustrotia*." McDunnough described *Nerastria* in 1937, and moved *albiciliata* to that genus in 1938. Most recently Franclemont and Todd, *in* R. W. Hodges *et al* (1983) placed *Nerastria* as a synonym of *Cobubatha* Walker (1863). Based on the charaters described below, I feel that *albiciliata* and the new species should be assigned to a separate genus.

## Allerastria R. M. Brown, new genus Type species: Yrias albiciliatus Smith, 1903

**Adult.** Head with eyes of both sexes large, round, greater in diameter than width of front; front (fig. 2, 4) with a rounded projection, scaling giving front a squared appearance when viewed laterally; labial palpi upturned, second segment nearly straight, paralleling front, third segment short, conical to middle of eye; antennae serrate in both sexes, males with ventral setae much

longer than in female, nearly equal to diameter of antennal shaft; male antennae with 50-57 segments, female 48-53 segments. Thorax robust, fore tibia with epiphysis arising approximately one-third distance from basal end of tibia in both sexes; epiphysis shorter in females; metathoracic tibia of males slightly swollen with long hair scales on the inner surface forming a vestigial hair pencil, both pair of spurs present. Abdomen slender in males, more robust in females, extending beyond hind wings, abdomen without dorsal tufts.

Fore wings longer than wide, apex angulate, outer margin rounded; Sc free, ending seven-tenths from base;  $R_1$  from discal cell;  $R_3$  anastomising with  $R_4$  forming an accessory cell;  $R_2$  from top of accessory cell;  $R_5$  from apex of accessory cell;  $M_1$  from bottom of accessory cell widely separated from  $M_2$  and  $M_3$ ; end of discal cell open;  $M_2$  and  $M_3$  from lower angle of discal cell,  $M_3$  closer to  $M_2$  than to  $CuA_1$ ;  $CuA_2$  arising from beyond middle of cell; 1A straight and free. Hind wing full and without angulation; Sc and R confluent for one-fourth of length of cell; R and  $M_1$  separate from upper angle of cell;  $M_2$  and  $M_3$  from lower angle of cell,  $M_3$  closer to  $CuA_1$  than to  $M_2$ ;  $M_3$  and  $CuA_1$  occasionally stalked;  $CuA_2$  arising from middle of cell; cell open; 1A and 2A straight and free.

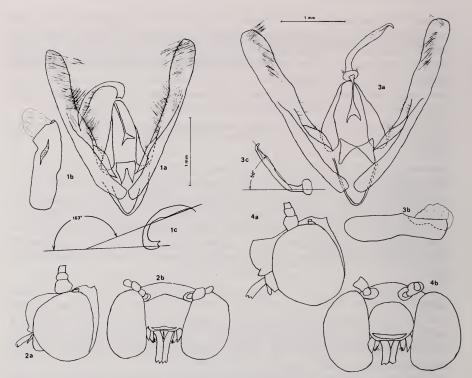
Male genitalia (fig. 1, 3). Valvae simple long, slender with parallel sides, length 6–7 times width; inner surface of valvae moderately setose; uncus long, tubular, down hooked, with lateral setae; scaphium long, slender, stalk with a widely bifurcated tip, area between tips roundly concave, scaphium length .55–.65 mm; juxta with basal margin deeply excavated; saccus, variable; aedaeagus 1.0–1.3 mm long, .25–.33 mm wide.

**Female genitalia** (figs. 5, 6). Corpus bursae round to oval, membranous, without signum; ductus bursae membranous, short; ostium with sclerotized collar; posterior apophyses shorter than anterior apophyses, length 0.4-0.5 mm to 0.75-0.8 mm; ovipositor lobes well developed, 0.7-0.8 mm in length, densely covered with setae.

Diagnosis. The species of Allerastria can be separated from those of Cobubatha Walker (1863) by a number of characters. In both sexes of Allerastria the front is projecting greatly beyond the eyes, but less so than in the genus Amiana Dyar (1904). The third segment of the labial palpi in Allerastria are short and conical, slightly longer than their diameter, where as in Cobubatha the length of the third segment is at least twice the diameter. The male antenna has the ventral setae much longer than in Cobubatha. The species of Allerastria, similar in color and maculation, have the median areas of the fore wings predominantly cream-white and differ from much of the Cobubatha species which have a dark brown median band on the fore wing. The male genitalia of Allerastria have the valvae long, narrow with parallel sides, in Cobubatha these structures broaden toward the apex and are not quite so long.

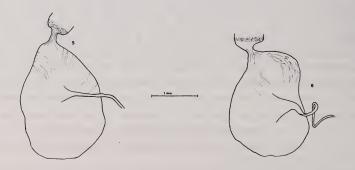
**Distribution**. *Allerastria* flies in the deserts of the southwestern United States, and the San Joaquin Valley, California. The majority of specimens used in this study are from southern California. The moths are on the wing from April through September.

**Etymology.** Allerastria is to read as another (allos) erastria and is feminine.



Figs. 1–2, Male genitalia. *Allerastria albiciliata*. 1a main body of genitalia; 1b aedaeagus; 1c degrees of uncus downflex. 2a head, left lateral; 2b front.

Figs. 3–4, Male genitalia. *Allerastria annae*. 3a main body of genitalia; 3b aedaeagus; 3c degrees of uncus downflex. 4a head, left lateral; 4b front.



Figs. 5-6, Female genitalia. Fig. 5 Allerastria albiciliata. Fig. 6 A. annae.

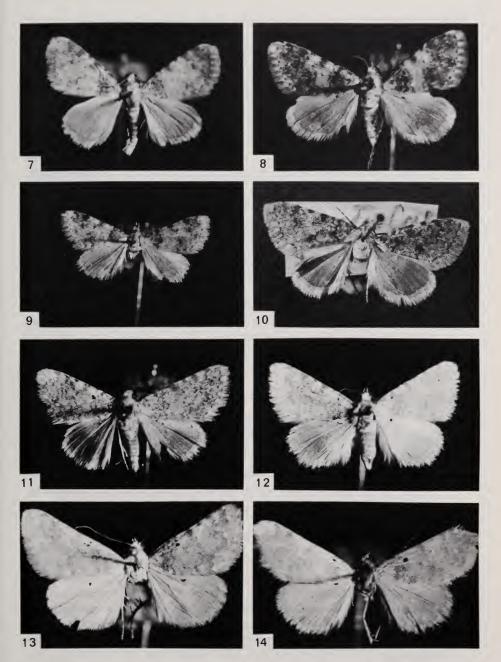


Fig. 7–14, Adults. Fig. 7 *Allerastria albiciliata albiciliata*, male. Fig. 8 *A. a. albiciliata*, female. Fig. 9 *A. a. paula*, male, Holotype. Fig. 10 *A. a. paula*, female, Allotype. Fig. 11 *A. a. chacoensis*, male, Holotype. Fig. 12 *A. a. chacoensis*, female, Allotype. Fig. 13 *A. annae*, male, Holotype. Fig. 14 *A. annae*, female, Allotype. Illustration 2 × natural size.

Key to Species,

## BASED ON MACULATION Underside wings prominently bicolored, basal half cream-white to 1a) white, distal half lead-gray to tan ..... 2a. Underside wings not as in 1a, uniformly colored cream-white ..... 1b) ..... annae n. sp. Small, fore wing length 9.0-10.0 mm, heavly suffused with 2a) brown scaling, from the San Joaquin Valley (Tulare Co.), California ..... albiciliata paula n. subsp. Larger, fore wing length 9.0-13.0 mm, from the southwestern 2h) (Arizona, Southern California, Nevada, and New Mexico) United States. Upperside fore wing white, tan or pink ............ 3a. Upper fore wing (length 9.0-11.0 mm) may or may not have a 3a) pink flush. Upper fore wing crossed with basal sub-terminal lines lead-gray. Median area varies from white to pink. Southern California, western Arizona and Nevada ..... ..... albiciliata albiciliata. Upper fore wing (length 11.0-13.0 mm) cream-white to tan with 3b) light brown scales scattered over wing. In well marked specimens brown scaling forms indistinct cross lines. No lead-gray color or ..... albiciliata chacoensis n. subsp. BASED ON MALE GENITALIA Uncus down flexed approximately 163° (fig. 1c) with heavy setae laterally arranged; juxta basal margin deeply excavated to near caudal margin (fig. 1a) ...... albiciliata. Uncus down flexed approximately 50° (fig. 3c) with fine setae 1b) laterally arranged; juxta with basal margine deeply excavated to caudal margin (fig. 3a) ..... annae n. sp. BASED ON FEMALE GENITALIA Ductus bursae nearly twice as long as wide; corpus bursae regularly oval; ductus seminalis rapidly narrows to straight tube leading to the right ...... albiciliata. Ductus bursae short, wider than long; corpus bursae irregularly 1b) round with right caudal quadrent roundly projecting, ductus seminalis broadly based and tapers to a spiraled tube leading to the right . . . . . . . . annae.

# Allerastria albiciliata albiciliata (Smith) new combination (figs. 1, 2, 5, 7, 8)

Yrias albiciliatus Smith, 1903, Trans. Amer. Entomol. Soc. 29:215-216. (TL: Yuma Co., Arizona)

Eustrotia bifasciata Barnes & McDunnough, 1912, Canad. Entomol., 44:218. (TL: La Puerta Valley, San Diego Co., California)

Nerastria albiciliatus, McDunnough, 1938, Check list of Lepid. of Canada and U. S. Amer. Part 1, Macrolepidoptera, Mem. So. Calif. Acad Sci., 108.

Cobubatha albiciliata, Franclemont & Todd, in R. W. Hodges et al., 1983, Check List of the Lepidoptera of America North of Mexico, p. 132.

The description of *albiciliata* by John B. Smith and the description of *Eustrotia bifasciata* by Barnes and McDunnough are sufficient to make further descriptions of maculation unnecessary. However, the genitalia of either sex has not been described.

Male genitalia (fig. 1). Valvae long, narrow, with slight constriction midway between base and apex, costa with long setae, apex rounded and clothed with long setae, sacculus and median ridge with short setae; saccus tapering to a blunt point; uncus (fig. 1c) sharply down-flexed with apical half slightly swollen, terminating in a sharp spine, long prominent setae laterally arranged; scaphium with apex widely bifercated, slightly concave between tips, narrowing to a long thin shaft to point of attachment; juxta with sides incurved, basal margin deeply excavated nearly dividing juxta in two, caudal margin straight; aedaeagus (fig. 1b) robust, armed with flat, narrow chitinous structure.

**Female genitalia** (fig. 5). Corpus bursae oval, without signum or other structures; ductus bursae membranous; ostium with narrow, lightly chitinized band at caudal opening of ductus bursae; bursae seminalis arising ventrally from moderately broad base, narrowing rapidly to a straight tube; posterior apophyses 0.5 mm long, anterior apophyses 1.0 mm long; ovipositor lobes well developed and densely covered with setae.

**Distribution.** Arizona: Coconino Co.; Maricopa Co.; Pima Co.; Santa Cruz Co.; Yuma Co. California: Imperial Co.; Inyo Co.; Kern Co.; Mohave Co.; Riverside Co.; San Bernardino Co.; San Diego Co. Nevada: Clark Co.

**Remarks.** Two hundred forty seven specimens (78 males and 169 females), 6 genitalic and 3 wing slides have been studied.

# Allerastria albiciliata paula R. M. Brown new subspecies (figs. 9, 10)

Male. Head cream-white with scattered gray-tan scales; antennae tan and gray checked. Thorax ventrally cream, dorsally cream with scattered gray scales; prothoracic tibia gray with middorsal cream-white spots, scales over epiphysis cream-white; tarsi gray with cream-white at joints; mesothoracic leg with longest spur 2.5 times longer than shorter; tibia dorsally gray with tufted middorsal cream-white scales; tarsi gray with cream-white at joints; metathoracic leg with two pair of spurs, longest upper spur 2.0–2.5 times longer than shorter; tibia cream-white with very little gray; tarsi light gray, cream-white at joints. Abdomen ventrally cream-white, dorsally gray with cream-white bands. Fore wing above with basal area cream-white with heavy overlay of gray scales; t.a. line sinuous, tan with basal border heavy gray, distal border less defined by gray scales; median area light tan, median band represented by a gray square on costa; t. p. line light gray, lightly outlined by dark gray scales, with white scales on the veins; subterminal area light tan; fringe with spatulate scales of various length, concolorous with subterminal area; fore wing

below shiny with inner half cream-white, outer half gray-white. Hind wing above, shiny, with inner half cream-white, outer half gray; below marked as above but with more color contrast. Fore wing length 9.0-10.0~mm.

Female. Slightly larger than male, with maculation the same.

Genitalia. As in nominate subspecies.

**Types.** Holotype, male, California (Tulare County), Exeter, 7–VI-1924, (R. M. B. slide #309). Allotype, female, California, (Tulare County), Exeter, 15–VI-? (R. M. B. slide #324). Paratypes, 3 males, same locality as types, data as follows; 5–IX-1924, R. Dodge; 18–VII-1924, R. Dodge; 15–VI-1940, E. A. Dodge. The types and paratypes are in the collection of the California Academy of Sciences, San Francisco, California.

**Distribution**. This moth is known only from the type locality and is on the wing from June to early September.

**Remarks**. Five specimens (4 males and 1 female), 4 genitalic slides and 1 slide of the wings have been studied.

Subsequent to the photograph (fig. 10) of the allotype, an *Anthrenus* sp. (Coleoptera: Dermestidae) devoured the thorax leaving only the head, legs and wings. These parts have been attached to paper supports and are still useable for identification. The abdomen is mounted on a slide as noted above.

No difficulty should be encountered in recognizing this subspecies; *paula* is the smallest and darkest taxon in this genus. The heavy brown overlay gives this moth a distinctive appearance.

**Etymology**. I am calling this moth *paula* because of its small size. The name is feminine.

# Allerastria albiciliata chacoensis R. M. Brown new subspecies (figs. 11, 12)

Male. Head cream-white with tan scales; antennae checked with tan; thorax cream-white, dorsally scattered with tan scales; prothoracic leg, tibia dorsally gray with cream-white band midlaterally, scales over epiphysis cream-white; tarsi gray with cream-white at joints; mesothoracic leg with longer spur 2.0 times longer than shorter spur; tibia dorsally scattered with gray scales, with middorsal cream-white tufted scales; tarsi gray with cream-white at joints; metathoracic leg with two pair spurs, longest spur 2.3-2.5 times longer than shorter spur; tibia cream-white with very little gray; tarsi dorsally gray with cream-white at joints; abdomen ventrally cream-white, dorsally with faint tan bands. Fore wing above, all lines weakly represented, ground color creamwhite with mixture of light and dark tan scales; costa with seven variable dark-tan checks; basal and t. a. lines variably present; subterminal area with heaviest concentration of dark-tan scales; subterminal line present and scalloped. Fringe cream-white with long spatulate scales, dark-tan checks at end of veins. Fore wing below, shiny with inner half cream-white, outer half tan. Hind wing below marked as fore wing below. Fore wing length 11-13 mm (Holotype, 11 mm).

**Female**. Simular in size and color with maculation less distinct than in male. **Genitalia**. As in nominate subspecies.

Types. Holotype, male, New Mexico, San Juan County, Chaco Canyon

National Monument, 2–VIII-1962, S. F. Wood. Allotype, female, New Mexico, San Juan County, Chaco Canyon National Monument, 3–VIII-1962, S. F. Wood, Paratypes, 3 males and 5 females. Same locality and collector as types, data as follows;  $1 \circlearrowleft 8-VII-1962$ ;  $1 \circlearrowleft 1 \circlearrowleft 17-VII-1962$ ;  $1 \circlearrowleft 2 \circlearrowleft 2-VII-1962$ ;  $1 \circlearrowleft 3-VIII-1962$ ;  $1 \circlearrowleft 6-VIII-1962$ . The types and paratypes are in the collection of the Los Angeles County Museum of Natural History, Los Angeles, California.

**Distribution**. This moth is only known from the type locality. It is on the wing in July and August.

Remarks. Ten specimens (4 males and 6 females), and two genitalic slides have been examined.

This moth can be seperated from the other subspecies by the general distribution of tan scales and extremely weak markings. The maculation of the fore wing is not divided into easly recognizable areas, although the tan scaling forms weak striations.

**Entymology**. I have named this moth after the Chaco Canyon National Monument to honor and point out the valuable role the national park system plays in preservation of the wildlife resource. For with out this great system and the many dedicated people the rare and unusual would have been lost long ago.

# Allerastria annae R. M. Brown new species (Figs. 3, 4, 6, 13, 14)

Male. Head (fig. 4) dirty cream-white; labial palpi upturned to above middle of eye with scattered lead-gray scales; antennae, lead-gray with white checks. Thorax dirty white with light pink tinge; collar and tegulae with most pink; prothoracic leg cream-white, tarsus lead-gray with white at joints, epiphysis three-fourths fore tibial length; mesothoracic leg marked as prothoracic leg; metathoracic leg marked as previous legs. Above fore wing with basal space bicolored, inner area concolorous with thorax, outer lead-gray; costal area above discal cell with two diffused white spots; t. a. line sinuous, lead-gray, basally edged with a few white scales, distally by rust-red; t. p. line lead-gray, basally shaded red, distally with lighter gray, t. a. line begins on costa, crosses to vein CuA<sub>1</sub>, accompanied by scattering of white scales forming a faint line, thence basad to median shade, turning then to inner margin; median area light gray-tan, divided in costal area by median shade. Subterminal line represented by white scales on veins, subterminal area tan with darker lunuals at vein ends. Fringe gray. Hind wing ground color concolorous to thorax, distal half with light gray shading. Fringe concolorous with thorax. Wings below unmarked, concolorous with thorax. Fringe on fore wing slightly darker than on hind wing.

**Female.** similar to male in maculation, the markings less contrasting.

Male genitalia (fig. 3). Valvae long, narrow with parallel sides; apex rounded, heavily clothed with setae on distal half, basally naked except for a small cluster of setae on low median ridge; saccus base square and one-third saccal width; uncus (fig. 3c) tubular, long, pointed, down-flexed, short fine setae laterally arranged; scaphium with apex widely bifurcated, deeply concave, narrowing to a long narrow shaft; juxta bifid, deeply excavated basally and apically appearing as two triangular units narrowly united; aedaeagus (fig. 3b)

robust, less than combined length of tegumen and saccus, without internal armature or spicules, posterior end produced into a shelf-like projection, dorsal surface heavily chitinized with short stout setae. Length three times diameter.

**Female genitalia** (fig. 6). Corpus bursae irregularly oval with a membranous projection on right caudal quadrent; ductus bursae short and asymmetrically placed; ostium with narrow chitenized band separated from caudal opening of ductus bursae; ductus seminalis arising ventrally from a very broad base and narrows to a spiraling tube. Apophyses short, not reaching ostium; ovipositor lobes well developed and densely covered with setae.

Fore wing length in holotype, 13.5 mm; allotype 13.0 mm; paratypes, 12-13 mm.

Types. Holotype, male and Allotype, female, California, Inyo County, Death Valley National Monument, western mouth Titus Canyon, elevation 1000 ft. (305 M), 6–IV-1977, Richard M. and Paula J. Brown. The genitalia of the holotype is mounted on R. M. B. slide #302, and the allotype is on R. M. B. slide #318. Paratypes, 2 males, 7 females, same locality and data as holotype. California: Inyo County; 1? Furnace Creek Death Valley, 10–IV-1931, G. Willett; 1? Triangle Springs Death Valley, 11–12-IV-1942, G. Willett; 1? Mesquite Springs Death Valley, 19–22-IV-1943, G. Willett; Riverside County; 1? Palm Springs, 21-IV-1920; San Bernardino County; 1? Baldy Mesa, 9-IV-1932, J. A. Comstock; 1? near Barstow, 10–V-1940, C. Ingham; 1? Yermo, 28-VI-1938; 1? Yermo, ?-IV-1939. The National History Museum of Los Angeles County, California will receive eight paratypes, one pair of paratypes to the National Museum of Natural History, Washington, D.C. The balance of the type material will be in the collection of the California Academy of Sciences, San Francisco.

**Distribution**. The desert regions of southern California. As more specimens are taken, it probably will be found to fly sympatrically with  $A.\ a.\ albiciliata$ . On the wing from April through June.

Remarks. Twenty two specimens (6 males and 16 females) and 8 slides of the genitalia were studied. This is an extremly variable species in maculation. It varies from nearly immaculate individuals to those like the well marked holotype. The first color to be lost is the rust red, the lead-gray band then fades but never completely disappears. *Allerastria annae* is very close to *albiciliata* in maculation but lacks the sharp definition of pattern found in *albiciliata*. *Allerastria annae* also has much less contrast between the light and dark areas of the hind wing than is found in *albiciliata*.

The male genitalia of annae can be told from those of albiciliata by the uncus being down flexed approximately  $50^\circ$  (fig. 3c). In albiciliata the scaphium has a long shaft with parallel sides, whereas in annae the sides gradually diverge to a widely bifurcated apex. Also annae can be separated from albiciliata by the deep basal excavation of the juxta found in annae which gives an appearance of two triangular units losely united.

**Etymology**. This moth is named after my wife, Ann, who has given so much in support and understanding. The name is feminine.

Acknowledgments. Special thanks to Robert W. Poole, National Museum of Natural History, for reviewing my specimens and the original manuscript, his confirmation of my conclusions and critical comments are greatly appreciated. I

am also indebted to Julian P. Donahue, National History Museum of Los Angeles, and to Paul H. Arnaud, Jr., The California Academy of Sciences, for without their generous loans of specimens this paper would have been much less comprehensive. Thanks to my wife, Ann, who produced the photographs used in this paper, and also to two anonymous reviewers who caused a great deal of work.

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## Observations on Problema bulenta

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The rare skipper, *Problema bulenta* (Boisduval and LeConte), is uncommonly observed and has never been photographed in nature. Here we report behavioral and flower use observations made in July, 1984 at Blackwater National Wildlife Refuge, Dorchester County, Maryland.

Previous nectar utilization has been reported by Jones (1926), who observed the species visiting pickerelweed (Pontederia cordata) in North Carolina and by Covell and Straley (1973), who reported bulenta visiting swamp milkweed (Asclepias incarnata) in Virginia. At the Maryland locality P. bulenta was fairly abundant and was observed by several persons, and as a result, more flower visiting observations were possible. The primary nectar source at Blackwater NWR was button-bush (Cephalanthus occidentalis). Secondary nectar sources observed were the two previously reported, swamp milkweed and pickerelweed, as well as red clover (Trifolium pratense) and dogbane (Apocynum cannabinum) (J. Fales, W. Grooms, R. Smith, pers. comm.).

In 1984, adults were seen from June 20 to July 14 — being most common later in the flight period. Our observations and those of J. Fales indicate that females are seldom seen at flowers and vary from 4 to 10 males seen for every female. Females may spend more time in the immediate vicinity of their host — suspected to be a large grass. Adults fly very close to the water at all times; most were seen within 30 cm. The highest above water was one seen 1.5 m. The flight is rapid, strong and noisy. Individuals seem to return again and again to the same area of a nectar plant. When visiting buttonbush these skipper usually visit low flowers preferring to rest on the under surface of the inflorescence, a site that is often in shadow. At the Maryland locality the wind blows almost constantly in variable gusts. The butterflies at flowers are constantly turning and moving from flower to flower. Flower visitation is from 10.00 to 15.00 hr; after that time the butterflies are no longer to be found.

Other butterflies sharing the buttonbush flowers with *P. bulenta* were *Epargyreus clarus*, *Erynnis horatius*, *Ancyloxipha numitor*, *Wallengrenia egeremet*, *Poanes viator* (abundant), *Phyciodes tharos*, and *Vanessa virginiensis*.

This skipper is very difficult to photograph. One must go into the river's water or stand at its muddy edge. This together with the almost constant wind, and the low, nervous flight of the insect makes such attempts trying at best.

The habitat is similar to that found along the Chickahominy River in Virginia (Covell and Straley, 1973). It seems likely the Maryland colony is univoltine as suggested by Opler and Krizek (1984). Further investigation is necessary to reveal the host plant and reproductive biology of this uncommon insect.

Acknowledgements. We thank John H. Fales, Calvert, Maryland; Richard Smith, Baltimore; and William C. Grooms, Tysons Corner, Virginia, for sharing their field notes on this butterfly.

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Figures 1–2. Adult *Problema bulenta* nectaring at buttonbush (*Cephalanthus occidentalis*) at Blackwater National Wildlife Refuge, Dorchester County, Maryland, on July 14, 1984.

1. Male, 2. Male.

### **Book Reviews**

THE BIOLOGY OF BUTTERFLIES. Symposium of the Royal Entomological Society of London, Number 11 (R. I. Vane-Wright and P. A. Ackery, Eds.). Academic Press, London, 1984.

Purchase the book if you take your lepidopterology at all seriously. That addresses the overall picture quite sufficiently. Of course, the thing is most certainly not without its peculiar flaws, although in fairness this review often deals with shortcomings inevitable in any such tome covering comparably broad terrain.

The butterfly symposium itself took place in September 1981 at the British Museum of Natural History, coincident with the eightieth year of Prof. E. B. Ford, in whose honor the event was dedicated. A star-studded cast of 44 signed off on the 33 articles ultimately shepherded to press by the capable hands of Vane-Wright and Ackery. The articles are organized into eight major areas of research on butterfly biology, which here seem most sensibly grappled with in the order in which they appear.

I. Systematics. Since this is a volume on butterfly biology, it is not surprising that butterfly taxonomy is allotted only minimal page space. Indeed, Ackery sequesters such considerations in but the first 13 pages of the total 429, with a healthy chunk of that devoted to recounting and judging faunistic works of the world. All in all, we hear relatively little about butterfly faunistics as compared to butterfly taxonomy (and, of course, bloated and imbalanced work on limited faunas seems to be the relentless vogue in the latter). Not so with Ackery's concise and bibliographic faunistic summaries — hats off to him for skipping the pedestrian, and pointing the way into an important yet often neglected literature.

**II. Populations and Communities.** This section contains two lengthy and two very brief articles. An Ehrlichian overview of population structure *sensu strictu* is both expected and appropriate in a volume of this stature, since the Stanford studies are among the forerunners. I've read essentially everything the Ehrlich group has put out over the years, and this is one of the most readable and widely appealing of their available reviews. More is known about population structure in *Euphydryas* than in most other species, and it is sobering indeed to hear Ehrlich berate his favorite creatures, and call for studies on a less biased taxonomic sampler of butterflies.

Gilbert then expands the focus to entire butterfly communities; given Ehrlich's caution, it is no surprise that generalizations are even fewer here. In short, the number of possible explanations for observed patterns increases explosively as one moves from single to multiple-species studies (infrataxonomic differences even notwithstanding). As a synopsis of this still nascent field Gilbert's article is fine. A gem within it is the paraphrasing of Munroe, who in his thesis had written the kernel of island biogeography well before it was popularized by MacArthur & Wilson's subsequent monograph. However, Gilbert quotes Munroe to establish a sad point, namely that "the slow progress of butterfly ecology [is because] . . . it has often been an afterthought of systematic or genetic studies."

The final two short articles in this section do not belong. Pollard's simply doesn't begin to do justice to the important field he has helped to engineer. Read his journal articles on relative abundance instead, and the terminal paper in the symposium volume. Morton's asks how the process of marking butterflies influences their subsequent activity. While there has never been much doubt that mark effects occur commonly, there are also few published studies addressing the issue. Morton's paper is generally helpful in this latter regard, but his data are useful only insofar as one tolerates the failure to measure catchability differences, and other factors central to analysis of recapture probabilities (see below).

III. The Food of Butterflies. This third section mirrors its predecessor in having two long and two short articles. Chew & Robbins lead off with one of the long ones, on egg-laying in butterflies. Their article embraces a large literature, hitting subtopics as diverse as oogenesis, selecting oviposition sites, and the evolution of oviposition specificity. Give them an 'E' for effort. It is partly the magnitude of their selected topic (too broad for one article), but mostly their choppy prose and superabundant citations which run the article aground. Large segments of the text are choked with 2–3 times as many references as necessary, and accordingly this is one of the more difficult to read among the symposium articles. Scan through it for the goodies to your liking. Their final section is probably the most provocative, and ushers in the notion of 'large-scale evolutionary jumps,' a subject taken up independently in other contexts by other authors in the volume.

Singer, whose writing is vastly clearer, addresses a restricted but closely related array of topics. He first reviews host discrimination by females, and then turns to the consequences of female choice upon (the essentially shipwrecked) larvae. A trademark of Singer's is careful scrutiny of intervening variables — what might loosely be described as the dozen or so factors you couldn't measure, but which your critics seize upon with glee. His trademark is evident throughout the latter half of this article (e.g., pages 85–87). It makes for tempered discussion, and, consequently, good reading.

At the end of this chapter are two more brief articles. Courtney's is scarcely a page, is merely a listing of homilies about habitat and footplant selection, and again does not belong in the volume. My advice is the same as for Pollard's effort in Chapter II: go read Courtney's fine original research papers instead. Edgar's short data paper marshalls believable evidence that plants in the family Parsonsiae represent ancestral foods for danaines and heliconiines.

IV. Predation, Parasitization, and Defence. This section contains a smattering of articles dealing with threats to butterflies — who eats them, where, when, and why, and the consequences in evolutionary time. Dempster asks the damaging question: what in fact do we know of the natural enemies of Lepidoptera themselves (cf. the abundant indirect evidence of their effects)? The essential lesson from his lead article is straightforward, and can't be emphasized enough — we know depressingly little about the influences of natural enemies on lepidopteran populations in the field. Lane's tantalizing short second article, on ectoparasitic midges on butterflies, only reaffirms Dempster's point (an excellent parallel treatise to Lane's is Treat's book on moth mites). In sum, our understanding of predators and parasites remains in 'seek and describe' mode.

These tentative articles give ground to Brower's methodical and exacting dissection of lepidopteran chemical defense. The longest of the Symposium articles, it is also among the best, a basic and refreshing subplot within it being re-categorization of the myriad terms applied in the literature on chemical defense and mimicry. Brower first establishes these theoretical constructs, and then marches into the fray and sorts through the booty of published, often fragmentary information. His differentiation between Class I (noxious) and Class II (innocuous) defensive chemicals becomes central to arranging the mess, and understanding the roles played by diverse assemblages of chemicals in the overall picture of chemical defense. Brower's attention to spatial and temporal diversity in predator behavior is similarly welcome. As with Singer, Brower has the keen eye for how to deal with observed variation in a systematic fashion.

Marsh et al.'s short article has the unenviable distinction of following Brower's and preceding Turner's. Their idea is laudable: test the anti-tumor action of various lepidopterous extracts. But the data are few (though interesting), and the recitations smack a little much of the narrow approach against which Brower just finished campaigning so successfully.

Turner opts for the moderator's stance, balancing opposing arguments while dismantling traditional dichotomies between Batesian and Mullerian mimicry. This he caps off with a lengthy and poignant discourse on saltational genesis of mimicry complexes. Indeed, by the end of the article, Turner has roamed fully into a general treatment of neo-Goldschmidtian punctuationalism (his tongue-in-cheek "evolution by jerks"). Throughout he draws upon the exemplar tropical heliconiine-ithomiine mimicry rings to bolster specific arguments. Turner's temperance helps to unravel the various concepts, and his article can certainly stake its claim as an educated precis on mimicry.

The reader must again endure two plus pages of the suboptimal after a masterpiece. In their introduction to the symposium, Vane-Wright et al. indicate that Gibson's automimicry article "generated much discussion . . . at the meeting." Within the walls of said meeting is where this off-the-cuff model should have stayed to ripen a bit. Field workers with an accompanying feel for modeling will have little difficulty flagging the several tenuous assumptions and their scant support from data. For automimicry, start with Brower et al. (1967), et seq., and work yourself forward through the literature from there.

V. Genetic Variation and Speciation. Leading off the second half of this volume is a variegated assembly of papers dealing with microevolutionary matters. Brakefield's is the principal article, a classical British ecological genetic investigation of spotting pattern in satyrines. He devotes the first ten pages to detailed and data-intense elaboration on the classification and heritability of these demure undersurface spots, and then traverses a shopping list of selective pressures potentially responsible for the geographic and populational variation in spotting.

The "boundary phenomonon" is certainly among the funkier discordant morphological patterns thrown by *Maniola*. The undersurface spotting regime of this butterfly shifts abruptly along a front only dozens of meters wide in southwestern England, and the front itself moves about in both time and space. There is still no overpowering explanation for this pattern, despite several decades of research. Brakefield somewhat belabors the ambivalent results with

this and other aspects of the *Maniola* story, but gets on track with his own thing — the spots as anti-predator devices, fluctuating selective pressures, and a healthy plea for populational work on the immatures.

Brakefield's plate of 119 'pressed' *Maniola* on pages 174–175 is a welcome sight. (It reminds me of the cabinets full of quite prostrate Gerould *Colias* who have cohabited over the years with me in my niche in the museum). More importantly, of course, it is just about the only visible affirmation in the symposium that properly executed morphological work has always been and will always continue to be central to good evolutionary study. This too often gets billed as an antiquated tenet, in this heyday of gelled and pureed creatures (and narrowly defined biochemical jobs in evolutionary biology, and divested museum holdings).

Kitching picks up on the subject of chopped butterflies in the second article, but only offers a breezy two cents' worth on his electrophoretic work on danaids, and the possible concordance between his data and the morpholgical cladistic treatments of Ackery & Vane-Wright. Of what value is that? Granted, there are concerns other than review articles when one is completing a doctoral dissertation, but what an apparently lost opportunity for a coming lepidopterist to publish some hot-off-the-press research in a major tome. So, why?

Gordon follows with a brief yet stimulating notion that mimicry (and possibly speciation) in each African Acraea is linked to dispersal, which in turn is linked to patterns of local extinction. Though he errs in the same manner as others throughout the symposium by equating differences in recapture probability entirely to one of its several confounding components (in this case, to dispersal), his continued pursuit of the subject should uncover some treasures.

Pierce wraps up with another short piece, but one which strikes an appropriate balance between the data presented and the conclusions drawn. The suggestion that lycaenids speciate more rapidly because of low deme sizes and selection by females for both foodplants and 'ant' plants is most plausible. We can also now add lycaenid larvae to the growing list of bizarre entomological edibles.

**VI. Sex and Communication**. This is the most mature chapter overall in the volume; and Silberglied's is easily the best paper in this chapter, being both provocative and scholarly in content *and* well written. Smith's is a close second, with the differences in approach and opinion between he and Silberglied appearing to be in large part semantic (or reflecting 'taxonomic scale,' cf. the Introduction).

Silberglied treats us first to Darwin's view on lepidopteran coloration and an accounting of its diversity, and then settles in on visual signals important in male and female communication, respectively. His take-home message is that female butterflies choose not on the basis of visible male colors, but rather on the basis of UV signatures and smells; he leaves us thinking along intrasexual lines for explanations of male butterfly colors.

Smith analyzes mate selection in *Danaus* and *Hypolimnas*, offering one of the better blends of data and discussion in the volume. A main thrust of his is distinguishing between random preferential mating, and assortative preferential mating. It remains to be seen whether Smith's complex findings are generalizable throughout Lepidoptera. However, Smith takes high marks among the 44 authors for his frequent admonishments about the inadvisable lumping of heterogeneous sub-classes of data, and the certainty of subsequent errors in interpretation.

Three shorties follow. Platt et al. offer a short data paper conclusively showing lack of differential mate selection in tiger swallowtail morphs. Vane-Wright notes, in particular, how male narcissism might be a unifying force for apparently equivocal and/or puzzling results in butterfly ethology. Finally, Clarke talks a little about sex-ratio distortions in gypsy moth and *Hypolimnus* broods.

The terminal paper, by Boppre, addresses the chemical aspects of communication among butterflies. Admittedly, much of our general knowledge of this subject comes from experiments with moths — with butterflies, it has been largely anecdotes, some major works notwithstanding. Boppre dutifully covers his material (androconia, pheromones, associated behavior, etc.) but in at least twice the number of words required.

VII. Migration and Seasonal Variation. Baker's is the primary paper in this Chapter of only vaguely related articles, offering a glimpse into what governs the movement of butterflies. His temporal frame of reference is substantially longer (lifespan) than that typical of published work on butterfly movement (days or so), and this imparts to Baker a different and healthy perspective. Indeed, he treats topics such as direction ratios that often never surface in more conventional mark-recapture studies, and it is encouraging to see such initial advances in a curiously neglected field (after all, butterflies fly, and so why don't we know more details about their travels than we do?).

From flight we jump inexplicably into study of seasonal polyphenism, cast in the light of genetic assimilation. Shapiro reworks a theme he has been publishing on vigorously for a decade, though in this paper he treats us to data from some new taxa. I agree with the editors that Shapiro's effort is heroic despite equivocal results; he is also a bigger man than most to confess at the end that "if ... [so], one need only invoke ordinary Darwinian selection to evolve polyphenism, and neither genetic assimilation nor anything more arcane is necessairly required." See his Figure 27.5 if you have doubts as to the genetic (cf. environmental) basis of polyphenism.

Chapter VII continues its schizophrenia by shifting to an illuminating short piece by Porter on larval basking, and its probable link with efficient digestive activity. Two more brief, descriptive polyphenism papers follow: McLeod on *Precis*; and Yata et al. on *Pieris* (the latter being of some intrigue since it treats polyphenism in the immature stages).

VIII. Conservation. Pyle is the acknowledged popularizer of lepidopteran conservation worldwide, and an article from him is obligatory. Here he focuses on the recent eruptions of Mt. St. Helens in western North America, and the influence this literally earth-shaking event had on butterflies in the area. Glean the more general of Pyle's points, since the data are necessarily scanty and inconclusive (the appropriate comparative pre-eruption lepidopteran research sadly doesn't exist).

The second article by Parsons examines the distribution, biology, and conservation problems faced by the world's largest birdwing butterfly. While Parsons talks about habitat loss (e.g., encroaching oil palm plantations) and factors affecting foodplant distribution, he unfortunately didn't give air time to an intriguing, tested, and successful option — 'butterfly farming.' This novel technique simultaneously eases commercial demand for specimens without impacting wild populations, puts cash into the local economy, and (probably most importantly) fosters local interest and commitment to the conservation

ethic. Parsons' repeated citing of internal agency documents on the matter of butterfly farming only makes one yearn further for an expose in the more accessible, true public record.

This brings us to the ultimate paper in the volume. And it is the denoument — a masterly review by Thomas of lepidopteran conservation efforts in temperate countries. I can't praise it enough. In fact, it is pointless for me to waste your time recapping it here, except to say that it shows pithy insight on all aspects of complex conservation issues, including: the acquisition and analysis of data on population changes, pinpointing the factors responsible for the observed changes, the associated political and sociological backdrops, and how these three avenues of inquiry are (or aren't) translated effectively into day-to-day conservation practice. He certainly doesn't shy away from flagging the dismal failures among the gamut of conservation attempts.

Thomas really does have a handle on the 'big picture,' and I strongly urge that his paper be read carefully, with an eye toward integrating the lessons of the other 32 papers into the unifying framework offered in the 33rd. It is a fitting wrap-up indeed for this symposium — lepidopteran conservation efforts have been gaining momentum during their formative period of the past two decades, and stand to mature in their own right during the remainder of this century.

### Commentary.

As you have gathered, the symposium articles fall broadly into two size (and content) classes — very brief reports of narrowly defined studies, and long review articles. The short reports are of inferior quality, and detract from the impact of the symposium volume as a whole. Why juxtapose notes of passing interest alongside more permanent, scholarly reviews? After all, we have journals for the express purpose of communicating such short notes (and journal referees to reject the bad ones).

Obviously, I don't feel these short notes at all served the editors' stated intention (page 1) of amplifying or highlighting accepted dogma or difficulties. Nevertheless, there are other factors which editors must weigh (such as affording equal air time to all participants in joint ventures). While one may dislike the schizophrenia imparted by the short papers, Vane-Wright and Ackery can't be held wholly accountable for problems inevitable when concatenating as many as 33 papers. Choppiness is one such unavoidable problem.

Leaving style aside, one large matter of substance glares at me through these several hundred pages of otherwise excellent lepidopterology. Why is it that mark-release-recapture takes it on the chin in this volume? I see much innuendo on supposed 'problems with MRR,' especially the business of marking itself, but little concrete offered in the way of justification, let alone alternative methodology.

It is telling that authors in this symposium make essentially no mention of Tabashnik's research on sulphur butterfly population structure, insofar as it applies to the theory and practice of MRR (nor do they speak of Begon's 1979 book). Tabashnik's 1980 paper, published in *Oecologia*, is the seminal work in recent years dealing with the partitioning of recapture probability into its biologically distinct components. Not one author attempted to break down recapture probability here, yet each tried to interpret recapture probabilities. There is little excuse for continued unthinking analysis of recapture probability as if it were a unified whole. Catchability and residence are different, they

*combine* to form recapture probability, and the distinction is paramount. Age structure is also easy to monitor (via wing wear), and it too is central, but again few authors bothered to report it.

These are unsettling omissions. I get the impression that this pooh-poohing of MRR is traceable in large part to the intermittent reports detailing detrimental effects of marking (as championed in part by Morton here, and others elsewhere). Really, though, so what if marking effects exist? They're present by definition. This begs for tempered investigation of their impact on populational parameters, not thoughts of rejecting MRR as the basis for measuring population size (the fact is that few have cared to ask critical questions in this area). Non-marking techniques certainly have their place, but they can't yet supplant MRR, and doubtfully ever will.

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BUTTERFLIES OF EUROPE, Volume 1, Concise Bibliography of European Butterflies, Otakar Kudrna, Editor, 1985. AULA-Verlag, Postflach 1366, D-6200, Luisenplatz 2, Wiesbaden 1, West Germany. 447 pp. DM 248 (series subscription price DM 216).

The Concise Bibliography is the first volume to be issued of the eight-volume BUTTERFLIES OF EUROPE series edited by O. Kudrna. Volumes 3-6 will discuss butterfly families, while vols. 2, 7 and 8 pertain to lepidopterology, ecology, and conservation of European butterflies.

This initial volume consists of approximately 6000 bibliographic entries in alphabetical order by author and relating to various aspects of European butterflies. The entries are numbered sequentially with a few alphanumeric citations. The volume begins with a five-page Preface and a five-page Introduction; an eleven-page Subject Index concludes the book. The citations included date from 1901 to 1983. References are provided to earlier bibliographies that cover publications prior to 1900.

The editor states in the Introduction that this volume is designed "... to serve the needs of all students of butterflies of Europe ..." regardless of their professional status. This work is not intended to be comprehensive. The citations listed were selected from a database of over 10,000 references compiled during the preparation of the series as a whole. Major taxonomic papers are included along with citations to treatises about ecology, distribution, conservation, etc. Full citations are provided with the use of standard abbreviations for journal titles.

The Subject Index allows the user to locate references on the basis of family, geographic region, genetics, anatomy, and many other classifications. It does not, however, permit the user to locate citations by genus or species. This is perhaps the only shortcoming of the book, and to include an index to genera and species would have increased the size of this volume considerably.

This book is well made with clear type and English text. It should be a valuable addition to the library of anyone interested in European butterflies.

Clifford D. Ferris, Bioengineering Program, University of Wyoming, P. O. Box 3295 University Station, Laramie, Wyoming 82071.

THE BUTTERFLY GARDEN: Turning your Garden Window Box or Backyard into a Beautiful Home for Butterflies.

Mathew Tekulsky. 1985. Harvard Common Press, Boston, ISBN 0916782-69-7. Price \$8.95 paperback.

This charming and broadly informative book is an excellent piece for serious lepidopterists to give their inquiring friends. Tekulsky, a professional writer, has written the book well, and, as a consequence of research conducted in the course of writing, has in fact now become an amateur lepidopterist.

Works like this represent a new generation of popular entomology through emphasis on observation and data-keeping, as opposed to the collecting mania and deadend museum ideology of earlier days. In terms of public awareness, such Weltanschauung should be cultivated as one's social responsibility, in addition to the joys of a scientific hobby. Butterflies are increasingly recognized as indicators of a world environment that is going to hell.

The factual material is general, as it must be, since the means of augmenting butterfly densities by gardening practise obviously differ between Los Angeles and Brooklyn. Nevertheless, a wide and thorough set of topics is covered from classification/life cycles, life zones, to courtship, migration, foodplants and nectar sources, and conservation. An emphasis on notetaking is a good point, and the bibliography and citation of resources are excellent. Bob Pyle wrote the well done introduction.

ENTOMOLOGY OF THE CALIFORNIA CHANNEL ISLANDS: Proceedings of the First Symposium.

Menke, A. S. and D. R. Miller. 1985. Santa Barbara Museum of Natural History, Santa Barbara, CA 93105. 178 pp. + 8 separate maps. Price \$20. paperback.

For anyone with an interest in island biogeography, as the concept is strictly applied to islands, the California Channel Islands are perhaps the best surveyed such areas in the world. This volume is the latest and most complete work to date. Of the animals censused, the Lepidoptera are the second best known group (after Orthoptera). Jerry Powell authored the principal paper on Lepidoptera. Although he defines the paper as a preliminary overview, it bears reading by all interested in patterns of distribution, citing problem areas as well as general findings plus a thorough bibliography. Larry Gall provides a neat paper on the initial recorded incursion of Strymon melinus onto Santa Catalina Island. The sole habitat of its close relation (sister species?) S. avalona. The paper provides a nice but too-brief lesson in morphological character analysis by numerical techniques of intraspecific variation and identification of potential phenetic hybrids. Scott Miller gives the introductory perspective. Five other papers cover Orthoptera, bees, Sphecids, mealy bugs, beetles and tiger beetles. Excellent detailed finescale maps of all islands are given in a separate envelope. My sole criticism lies in the reproduction of typescript. Even though very well done in this case, there is something psychologically ephemeral about non-typeset work.

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Manuscript Format: Two copies must be submitted (xeroxed or carbon papered), double-spaced, typed, on 8½ x 11 inch paper with wide margins. Number all pages consecutively and put author's name at top right corner of each page. If your typewriter does not have italic type, underline all words where italics are intended. Footnotes, although discouraged, must be typed on a separate sheet. Do not hyphenate words at the right margin. All measurements must be metric, with the exception of altitudes and distances which should include metric equivalents in parenthesis. Time must be cited on a 24-hour basis, standard time. Abbreviations must follow common usage. Dates should be cited as example: 4. IV. 1979 (day-arabic numberal; month-Roman numeral; year-arabic numberal). Numerals must be used before measurements (5mm) or otherwise up to number ten e.g. (nine butterflies, 12 moths).

Title Page: All papers must have the title, author's name, author's address, and any titular reference and institutional approval reference, all on a separate title page. A family citation must be given in parenthesis (Lepidoptera: Hesperiidae) for referencing.

Abstracts and Short Papers: All papers exceeding two typed pages must be accompanied by an abstract of no more than 300 words. An additional summary is not required.

Name Citations and Systematic Works: The first mention of any organism should include the full scientific name with author (not abbreviated) and year of description. New descriptions should conform to the format: male: female, type data, diagnosis, distribution, discussion. There must be conformity to the current International Code of Zoological Nomenclature. We strongly urge deposition of types in major museums, all type depositions must be cited.

**References:** All citations in the text must be alphabetically listed under Literature Cited in the format given in recent issues. Abbrevations must conform to the *World List of Scientific Periodicals*. Do not underline periodicals. If four or less references are cited, please cite in body of text not in Literature Cited.

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# THE JOURNAL OF RESEARCH ON THE LEPIDOPTERA

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# Distribution and Abundance of Butterflies in the Urbanization Zones of Porto Alegre, Brazil

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Abstract The distribution of butterflies in the urban area of Porto Alegre was analysed by means of transects of avenues and data collected over a grid of 111 observation points. Maps were drawn showing the urbanization zones of the city, percent of vegetation cover as well as the distribution of 29 butterfly species. Three zones with relative uniformity can be identified along the urbanization gradient: B (buildings higher than four stories), vegetation cover below 20%; HB (houses and buildings of less than four stories), vegetation cover between 20 and 40% and H (houses, also including open areas within the city), vegetation cover above 40%. The distribution of butterflies in the city showed a life zone pattern very well correlated and oriented with the urbanization gradient. The border between zones H and HB represented a barrier for several species strongly associated with woods or natural fields, representing the most important transition area in the city fauna. The increase in the urbanization and pollution was accompanied by a decrease in the number of species and individuals registered as well as by a homogenization in butterfly distribution. In terms of abundance and distribution of its individual elements, the butterfly community of Porto Alegre is consistently structured in accord with the urbanization gradient, represented as distance from the center of the city. The predominance of this parameter is probably due to the fact that this distance is the main conditioner of many variables which are important for butterflies (such as urban climate, percent vegetation cover, air pollution and human density). Species of open areas, with high vagility, nectar feeders and with larvae feeding on exotic cultivated plants are dominant in the city.

### Introduction

Among the more esthetically pleasing animals which inhabit urban ecosystems along with man, birds and butterflies have high ranking. Few authors have attempted to investigate the determinants of butterfly occurrence and non-occurrence in man-made environments; most publications about butterflies in urban areas simply report a list of species found in a given city. In a more in-depth study, Shapiro & Shapiro (1973) studied the Staten Island (USA) butterfly community and called attention to its homogeneity. The butterflies found in abandoned lots, always the same, were increasing in number and distribution while the native and specialized forms were declining. The first

group included vagile colonizers with a high reproductive rate, feeding on weeds and probably tolerant of air pollution. Yamamoto (1977) studied the butterflies of Sapporo (Japan) and found that most of the individuals belonged to a small number of species; a decline in the butterfly fauna paralleled the increase of urbanization. Species of open areas, which hibernate during the pupal stage and reproduce three or more generations per year, were those more resistant to urbanization. His results showed the substitution of forest species by open area species. Singer & Gilbert (1978) offered some general theoretical considerations about butterfly ecology in urban environments.

In this work the entire urban area of Porto Alegre (Rio Grande do Sul, Brazil) was sampled for butterflies. The main objectives were to investigate butterfly distribution over the urbanization gradient and the influence of habitat variables on butterfly abundance.

### **Study Area**

The city of Porto Alegre is located in southern Brazil ( $30^{\circ}02'$  S,  $51^{\circ}14'$  W), with a population of over a million inhabitants. The altitude varies from 4 to 300 m above sea level (mean about 80-100 m). The region has a temperate-subtropical climate with high humidity and moderately high temperatures in the summer. The annual mean temperature is  $13.8^{\circ}$ C and the average rainfall 1322 mm.

The city is surrounded by agrarian ecosystems to the north, south and east; to the west are found the aquatic ecosystems of Guaiba River (Figure 1a). Within the city are found only remnants of woods in hard-to-reach places in the southern sector, where urbanization has been partially stopped. A field vegetation, either managed or abandoned, presently predominates on the periphery of the city.

Over a 1:20.000 city map was laid a 5-cm grid (equal to 1 km² real size). Using the geometric center of each square, 111 circles 3 cm in diameter (300 m radius or 0.283 km² real size) were defined. The circles corresponded to sampling subunits called observation points (OP). The distance of each OP from OP  $E_5$  (Figure 2) in the center of the tall building zone was considered "distance from the center of the city". The mean altitude of each OP was estimated as the arithmetic mean between its highest and lowest points. Over a 1:8.000 photograph of each OP was laid a  $6 \times 6$  cm square of millimetered paper (0.2304 km² actual area). The parts covered by plants, including native vegetation as well as lawns, back yards, vacant lots and street trees, were shaded. The calculated percentage of vegetation cover of each OP was extrapolated to the area of 1 km² (Figure 1b).

By examination of 1:20.000 aerial photographs of the city with the aid of a stereoscope, three zones of different intensities of urbanization could be drawn over a political map at the same scale: high (buildings zone or zone B; vegetation cover below 20%; zero to 2 km distant from

the center of the city), medium (houses and buildings zone or zone HB; vegetation cover between 20 and 40%; 2 to 7 km distant from the center of the city) and low (houses zone or zone H; vegetation cover above 40%; 4 to 12 km distant from the center of the city). The borders of the zones were adjusted by examination *in loco*. The final map (Figure 1c) was simplified to polygons, by drawing tangential lines to the borders of the different zones of urbanization (Figure 1d).

The radial arrangement of the main avenues of Porto Alegre has determined an urbanization gradient also radial and relatively similar in all directions from the center of the city. Over the urbanization gradient is found a complementary gradient of vegetation covering, also with a radial aspect and similar preferential orientation (northeast-southeast) (Figure 1b).

Zone B and industrial and shopping areas generally show less than 20% plant cover. Zone HB has under 40% plant cover, showing a close spatial relationship with the 15-30% class in Figure 1b. Zone H has in general plant cover value over 40%, reaching a maximum of 78%. The mean value was 39.3% (s = 17.2). The minimum value for this variable was 7.2% in OP E<sub>4</sub>.

### Methods

The distribution of butterflies was investigated using two methods: transects, and data recording in observation points.

### **Transects**

Four transect routes were used (AB, CD, EF and GH), along the main avenues out from the center of the city. The censuses began at 10 a.m. at the inner end of each route, and consisted of a round trip to the outer end and back. Ten such censuses were done along each route. All butterflies seen by naked eye were registered, whether flying or sitting up to 10 meters back from the street side of the buildings. The location of each individual was determined in relation to the nearest cross street.

## **Data Recording in Observation Points**

The whole set of the OPs was explored during three sampling periods (November-December 1980, March-April 1981 and June-July 1981). In each of these periods the OPs were visited sequentially, five per day. First the OPs of row 7 were visited followed by rows 8, 6, 9, 5 and thus successively (Figure 2). In each OP, a 45-minute period was spent constantly walking the streets and recording the number of individuals of different butterfly species seen. The field data were transferred to computer cards and all calculated values were obtained through the use of SPSS (Nie et al., 1975) programs.

### **Results and Discussion**

## Distribution of Butterflies along the Transect Routes

Table 1 includes the total number of individuals of different species along the four transect routes. The recordings for the final 1.6 kilometers of route AB (8 km in total length) are not included in this table, since they represent extra-urban data, not comparable to those obtained for other routes. Figures 3, 4, 5 and 6 show graphic representations of the butterfly groups along the four routes.

From AB to GH there occurs a levelling of topography, an increase of urbanization intensity and a decrease in the number of individuals recorded per km of transect (Table 1).

Dryas iulia, Ascia monuste orseis and Phoebis philea were the most numerous butterflies, totalling 30% of the recorded insects along each route. The predominance of these species is due, among other factors, to their great abundance in the region (including within the city), speed and mobility, and the vivid colors of their wings which allows easy spotting.

Table 1. Butterflies observed along 20 transect (center-suburbs-center) on four acess routes. Explanation in the text.

	AB CD				U T E F	Н				
SPECIES		.3)*		1.7)		1.9)		0.5)	TO	TAL
SPECIES	N	%	N.	%	N.	%	N	%	N	%
Dryas iulia (Fabricius, 1775)	88	17.0	63	14.3	46	12.9	26	9.9	223	14.
Ascia monuste orseis (Latreille, 1819)	65	12.5	55	12.4	49	13.8	32	12.2	201	12.
Phoebis philea (Johansson, 1763)	44	8.5	45	10.2	47	13.2	21	8.0	157	9.
Anartia amathea (Eschscholtz, 1821)	23	4.4	24	5.4	22	6.2	49	18.7	118	7.
Papilio scamander Boisduval, 1836	22	4.2	27	6.1	25	7.0	15	5.7	89	5.
Phoebis spp.	21	4.0	22	5.0	23	6.5	17	6.5	83	5
Junonia evarete (Cramer, 1779)	25	4.8	19	4.3	16	4.5	21	8.0	81	5
Colias lesbia pyrrhothea (Hübner, 1823)	29	5.6	34	7.7	1	0.3		-	64	4
Tatochila autodice (Huebner, 1818)	30	5.8	14	3.2	9	2.5	1	0.4	54	3
Papilio anchisiades capys Huebner, 1809	30	5.8	15	3.4	8	2.2		-	53	3
Urbanus spp.	16	3.1	13	2.9	13	3.6	8	3.1	50	3
Actinote spp.	6	1.2	18	4.1	7	2.0	13	5.0	44	2
Euptychia spp.	6	1.2	4	0.9	14	3.9	16	6.1	40	2
Anosia gilippus (Cramer, 1775)	22	4.2	6	1.4	8	2.2	2	0.8	38	2
Agraulis vanillae maculosa (Stichel, 1907)	3	0.6	8	1.8	13	3.6	8	3.1	32	2
Eurema spp.	9	1.7	6	1.4	10	2.8	î	0.4	26	1
Phyciodes spp.	2	0.4	5	1.1	9	2.5	8	3.1	23	i
	12	2.3	3	0.7	2	0.6	_	3.1	17	i
Battus polydamas (Linnaeus, 1758)	9	1.7	5	1.1	1	0.8	2	0.8	17	i
Eunica margarita (Godart, 1822)	2	0.4	8	1.8	4	1.1	_	0.0	14	ó
Dione juno (Cramer, 1779)							1	0.4		0
Methona themisto Huebner, 1818	8	1.5	3	0.7	1	0.3		0.4	13	0
Papilio hectorides Esper, 1794	3	0.6	5	1.1	2	0.6	2	_	10	ő
Biblis hyperia (Cramer, 1779)	3	0.6	_		4	1.1		0.8	9	0
Papilio thoas brasiliensis Rothschild & Jordan, 1906	5	1.0	2	0.5	-	_	1	0.4		
Placidula euryanassa (Felder, 1860)	-	_	4	0.9	1	0.3	3	1.1	8	0
Adelpha spp.	_	_	4	0.9	3	0.8	1	0.4	7	0
Heliconius erato phyllis (Fabricius, 1775)	2	0.4	3	0.7	1	0.3	1	0.4	7	
Dryadula phaetusa (Linnaeus, 1758)	1	0.2	1	0.2	2	0.6	4	1.5	6	0
Siproeta stelenes (Linnaeus, 1758)	1	0.2				0.8	- 1	0.4	5	
Papilio astyalus Latreille, 1819	4	0.8	1	0.2	- 7	_	-	-	5	0.
Diaethria spp.	1	0.2	3	0.7	1	0.3	-	_		0.
Doxocopa laurentia (Godart, 1821)	3	0.6	1	0.2	-	_	-	-	4	0
Hamadryas amphinome (Fruhstorfer, 1916)	2	0.4	2	0.5	-		-		4	0
Anaea itys (Gmelin, 1791)	1	0.2	1	0.2	1	0.3	1	0.4	4	0.
Dismorphia spp.	2	0.4	-		2	0.6	-	-	4	0.
Hamadryas spp.	2	0.4	1	0.2	-	-	-	-	3	0
Epiphile huebneri Hewitson, 1861	-	-	1	0.2	2	0.6	-		3	0
Heliopetes omrina (Butler, 1870)	-	-	-	-	1	0.3	2	0.8	3	0
Eurema deva deva (Doubleday, 1847)	1	0.2	1	0.2	-	-	1	0.4	3	0
Opsiphanes invirae Stichel, 1901	1	0.2	2	0.5	-	-	-	-	3	0
Dynamine myrrhina (Doubleday, 1849)	1	0.2	***	-	-	-	1	0.4	2	0
Riodina lysistrata (Berg, 1896)	-	-	1	0.2	-	-	1	0.4	2	0
Praepedaliodes phanias (Hewitson, 1861)	1	0.2	-	-	1	0.3	-	-	2	0
Mechanitis lysimnia (Fabricius, 1793)	2	0.4	-	-	-	-	-	-	2	0
Furyades corethrus (Boisduval, 1836)	1	0.2	-	-	-	-	-	-	1	0
Pyrgus oileus (Stoll, 1790)	1	0.2	-	-	-	-	-	-	1	0
Pyrgus communis (Giacomelli, 1928)	-	-	-	-	-	-	1	0.4	1	0
Doxocopa kallina (Staudinger, 1886)	1	0.2	-	-	-	-	-	-	1	0
Vanessa braziliensis (Moore, 1883)	1	0.2	-	-	-	-	-	-	1	0
Marpesia petreus (Cramer, 1776)	-	-	1	0.2	-	-	-	-	1	0
ypanartia bella (Fabricius, 1793)	-	-	_	-	1	0.3	-	-	1	0.
Philoros rubriceps opaca (Boisduval, 1870)	-	-	-	-	-	-	1	0.4	1	0
Others	7	1.3	11	2.5	3	0.8	-	-	21	1
Total	519	100.0	442	100.0	356	100.0	262	100.0	1579	100

<sup>\* (</sup>N/Km/TRANSECT)

The papilionids (Figure 3) show a reduction in the number of individuals from AB to GH; in the latter transect, except for one individual of *Papilio thoas brasiliensis*, all those recorded belonged to the species *P. scamander scamander*. This monotony is in accord with the small number of species of this family observed in the OPs located in this area of the city.

The sap and fruit eating nymphalids were most common along AB, also decreasing in the direction of GH (Figure 6). All these species are native of subtropical woods on the city periphery, showing their greatest numbers on the distal end of AB, which crosses areas with remnants of this habitat.

Along the routes AB, CD and EF the different families and subfamilies showed a sharp reduction of the species number and individuals inside the limits of zone B; only one or two species were recorded for each group of butterflies. On GH, however, there was a greater homogeneity in the distribution of these groups, represented all along the route by the species that on other routes were well represented in zone B. This emphasizes the environmental stress of this region. The homogeneity in the distribution of the different groups of butterflies along GH is probably due in part to the spatial uniformity of this portion of the city. This area has a very regular disposition of streets, similar to a chessboard, and is extremely flat with elevations below 5 meters, which represents a low diversification of habitats. In aerial photographs it shows great similarity among its different sites. The scarcity of vegetation on the margins of route GH tends also to increase the homogeneity in the distribution of butterflies, since it eliminates a factor of concentration of these insects. Farrapos Avenue, the greatest part of route GH, is surely the avenue with the greatest air pollution in the city due to particles and industrial gases as well as from vehicles. Pollution is a factor of homogenization of environmental conditions consequently decreasing the complexity of animal and plant communities belonging to a certain biotope. Thus, the smaller species number and homogeneity of distribution found along GH may also be explained by the air pollution in this area.

## The Urban Community of Butterflies

The data in Table 2 show the large number of individuals of a small number of butterfly species in the urban area. The data provide evidence that the butterfly communities of Porto Alegre are organized with a consistent structure. This can be seen from the results of the two methods used. For example, the more abundant species in the transects and OPs hold the top positions in the abundance ranking in the majority of routes and regions of the city (Tables 1 and 2). The majority of the genera and species which represent less than 2% of the records in the transects maintain this low proportion also in the OPs. It will be

Table 2. Total number of butterflies observed in 11 regions of the city of Porto Alegre.

PECIES							REGI						
		11	Ш	IV	V	VI	VII	VIII	IX	×	ΧI		
Ascia monuste orseis (Latreille, 1819)	117	100	111	138	102	80	90	80	58	70	65	EN 1011	% 8.7
Oryas iulia (Fabricius, 1775)	152	145	96	154	120	56	109	62	37	26	17	974	8.3
Junonia evarete (Cramer, 1779)	44	46	122	62	83	70	99	64	110	44	48	792	6.8
Jrbanus spp.	49	116	117	69	74	64	80	61	59	33	30	752	6.4
Fatochila autodice (Huebner, 1818)	63	84	55	57	74	55	47	43	45	30	30	592	5.1
Phoebis philea (Johansson, 1763)	76	86	60	57	43	29	67	62	12	39 43 53 26	22	557	4.8
Papilio scamander Boisduval, 1836	23	48	94	13	34	23	62	51	72	43	41	520	4.4
	23	48	84	13	64	29 23	02	20	72	53	41		
apilio anchisiades capys Huebner, 1809	66	73	84	48 28	64 70	23	39	30	37	26	15	505	4.3
ctinote spp.	45	67	93	28	70	16	69	25 34	7	12	2	434	3.7
graulis vanillae maculesa (Stichel, 1907)	47	67	54	47	59	59	21	34	11	17	6	422	3.6
Inosia gilippus (Cramer, 1775)	21	34	46	45	30 38	23	44	62	40	49	11	405	3.4
hoebis spp.	62	61	51	37	38	27	37	40	12	14	7	386	3.3
urema spp.	29	36	45	36	38	35	24	41	21	5	1	311	2.6
lattus polydamas (Linnaeus, 1758)	42	26	48	50	41	19	36	16	12	8	1	299	2.5
uptychia spp.	64	31 21	28	15	25 7	27	22	17	19	8	2	258	2.2
Inartia amathea (Eschscholtz, 1821)	24	21	33	10	7	46	13	56	11	15	12	248	2.1
apilio astyalus Latreille, 1819	17	22	31	33	22	10	15	12	25	7	2	196	1.6
feliopetes omrina (Butler, 1870)	18	21	21	12	19	30	17	28	11	3	4	184	1.5
eptotes cassius (Cramer, 1775)	19	24	20	36	19	3	25	9	10	10	6	181	1.5
Papilio thoas brasiliensis Rothschild & Jordan, 1906	15	18	15	13	18	12	25 22	13	15	13	10	164	1.4
Methona themisto Huebner, 1818	26	16	11	14	13	5	10	16	10	18	10	156	1.3
remona memisto nuebner, 1818	20	5	49	6	12	20	10 17	10	19	16	10 8 3	154	1.3
anessa braziliensis (Moore, 1883) hyciodes claudina (Eschscholtz, 1821)	26	10	49		12		17	16 12 3	3	16	2	134	
nycioaes ciauaina (Eschscholtz, 1821)	24	18	24	19	28	5	7	3	3	6	2	139	1.3
uryades corethrus (Boisduval, 1836)	19	8	50	17	12	21	6	4	-	1	-	138	1.1
apilio hectorides Esper, 1794	5	7	25	9	26	24	17	13	1	3	-	130	1.1
leliopetes alana (Reakirt, 1868)	12	10	25	15	23	14	8	12	1	1	5	126	1.0
urema deva (Doubleday, 1847)	8	12	12	11	12	28	9	16	5	6	-	119	1.0
lione juno (Cramer, 1779)	12	10	7	11	14	6	16	7	9	10	2	104	0.9
lione juno (Cramer, 1779) yrgus oileus (Stoll, 1780)	8	13	13	12	20	17	5	1	6	3	2 5 5	103	0.8
unica margarita (Godart, 1822)	29	9	9	10	5	7	8	4	1	6	5	93	0.8
eliconius erato phyllis (Fabricius, 1775)	33	4	4	12	15	7	10	1	3	1	1	86	0.1
arides perrhebus (Boisduval, 1836)	19	6	4	4	13	4	9	3	3	-	2	66	0.9
yrgus communis (Giacomelli, 1928)	2	8	12	9	14	7	ĭ	7	2	_	ĩ	63	0.9
olias lesbia pyrrhothea (Hubner, 1823)	- 1	2	3	4	1			á	38	_	4	61	0.1
uptoieta hortensia (Blanchard, 1852)	3	7	21	2	8	້		3	1	1		56	0.4
lamadryas spp.	18	6	- 1	6	10	5 3 2	5 2 3	2		i	3	51	0.4
ryadula phaetusa (Linnaeus, 1758)	4	18	6	1	10	9	2	1		2	1	45	0.3
ryadula phaetusa (Linnaeus, 1756)	6	8	3	9	_	1	4	1		2	i	42	
lacidula euryanassa (Felder, 1860)		4	2		9		2	2	2	1		42	0.3
ynamine myrrhina (Doubleday, 1849)	10		2	3	3	-				1	2	29 26	0.2
naea itys (Gmelin, 1791)	3	5	8	1	1	-	5	1	-	-	2		0.2
Parides agavus (Drury, 1782)	21	-	-	-	3	_	-	_	~~	-	-	24	0.2
delpha spp.	9	4	1	1	1	3		2	-	-	-	21	0.1
hiloros rubriceps opaca (Boisduval, 1870)	- 1	2	3	4	3	1 2	3	2	-	1	1	21	0.
iblis hyperia (Cramer, 1779)	9	- 1	3	1	-	2	1	2	-	1	-	20	0.1
urytides lysithous (Huebner, 1821)	6	3	1	4	4	1	1	-	-	-	-	20	0.
raepedaliodes phanias (Hewitson, 1861)	6	6	1	1	2	_	-	2	1	-	-	19	0.
haethria spp.	7	2	2	1	-	2	-	1	-	-	1	16	0.
hyciodes ithra (Kirby, 1900)	3	2	1	1	1	-	2	3	1	-	1	15	0.
iodina spp.	2	1	-	3	1	2	3	1	-		1	14	0.
ismorphia spp.	4	1	3	2	2	_	_	1	-	-	1	14	0.
loxocopa laurentia (Godart, 1821)	3	4		2		1	-	1	-	-	-	11	0.0
attus polystictus (Butler, 1874)	10	_	_	_	1	-	_	_	_	-	_	11	0.0
iproeta stelenes (Linnaeus, 1758)	. 2	2	1	_	3	_	***	2	-	_	-	10	0.0
iproeta stelenes (Linnaeus, 1758) osia angulosa (Walker, 1854)	7		-	1	1	-	_	-	-	_		9	0.0
ypanartia bella (Fabricius, 1793)		2		-	2	1	1	1	1		_	8	0.0
lamadryas amphinome (Fruhstorfer, 1916)	2	-	2	1	-	i		i	-		-	7	0.0
oxocopa kallina (Staudinger, 1886)	2	1	2	,		i	1				_	7	0.0
	2							_	3	1	_	6	0.0
psiphanes invirae Stichel, 1901	-	1			_	_	1	_				6	
arides anchises nephalion (Godart, 1819)	1	-	_	1	3	-	-	_	1	_			0.0
haloe cruenta (Huebner, 1823)	5		_	_	-	1	-		-	_	_	6	0.0
Itetheisa ornatrix (Linnaeus, 1758)	-	-	-	-	3	1	1	-	-	-	-	5	0.0
rittwitzia hymenaea (Prittwitz, 1865)	2	-	-	-	-	-	-	-	-	2	-	4	0.0
hyciodes lansdorfi (Latreille, 1820)	-	-	-	-	-	-	1	1	1	-	1	4	0.0
iproeta trayja (Hübner, 1823)	1	1	-	***	1	-	1	-	-	-	-	4	0.0
farpesia petreus (Cramer, 1776)	1	-	-	1	-	-	1	-	-	-	-	3	0.0
forpho catenarius Perry, 1811	3	-	-	-	-	-	_	-	-	-	-	3	0.0
nartia jatrophae (Johansson, 1763)	_	-	_	1	_	1	_	_	-	-	-	2	0.0
Philaethria wernicket (Röber, 1906)	2	-	-	-	_		_	_	_	_	_	2	0.0
Macrocneme chrysitis (Guerin, 1843)	-	-	1	-	1	_	_		_	_	_	2	0.0
piphile huebneri Hewitson, 1861	1	1									_	2	0.0
piphile huebneri Hewitson, 1861 Others	40	33	34	38	40	39	29	30	35	7	11	336	2.
uners	40	33	34	38	40	39	29	30	35		- 11	330	2.0

\* moths

shown below that this consistent organization may also be applied to the distribution of the members of this fauna.

Figures 7–10 show the distribution of the different groups of butterflies in the urban zones. These maps may be seen as an estimate of the distribution areas of different species in the urban area of Porto Alegre for the period of 1980–81; this is certainly suffering gradual modifications, considering the velocity of vertical and horizontal urbanization.

Within each subfamily or genus of butterflies there are species spread out over all zones of urbanization and others found in semi-circular bands progressively narrower and farther from the zones B and HB having as virtual center zone B. This fact is related to the radial character of the urbanization gradient and vegetation covering of the city. The majority of the species show a continuous distribution over the city, decreasing in amplitude towards more intensively urbanized zones. This, along with the high degree of vagility of the dominant

species (and the majority of others) discourages the use of the expression *mosaic distribution* (often applied to soil insects) for the butterfly fauna of Porto Alegre. The expression *life zones* introduced by Merriam (1894) to designate the changes of plant communities due to altitude and latitude better characterizes the zonation of the butterfly distribution on the urban gradient.

Each species shows a more or less similar distribution pattern in the three samples, though some members of the subfamily Nymphalinae reveal seasonal variations in their distribution. In each case the pattern of distribution verified in the transect routes was in general similar to the one found for the OPs. The species that showed a rather wide distribution in the OPs (such as P. scamander, A. m. orseis and D. iulia) also showed a wide distribution along the routes of transects. The species with a more restricted distribution in the OPs such as P. a. astyalus, P. hectorides and H. e. phyllis were found to be more frequent on the outer portions of the routes. The species observed only on the border of urban area (B. polystictus, P. a. nephalion and P. agavus), within areas not reached by the majority of the routes were very infrequent along the transects. Neverthless, they were found on the distal end of route AB which reaches the city periphery. These facts emphasize the zonation of distribution areas of butterflies in the urban area of Porto Alegre.

The species that were rare in the urban area (less than 1%) in general are stenotopic in the sense of the adult being typical of field or woods. They feed in the larval stage on native plants which are infrequent or non-existent in the city. Their distribution was restricted to peripheral portions of zone H, especially in the southern sector which is richer in remnants of subtropical woods and is nearer the granitic hills of the city periphery, where still denser woods are located. In the adult stage fruit and sap feeding is predominant.

In the central areas of the city, species of open areas predominate, in accord with the results of Yamamoto (1977) on the butterflies of Sapporo (northern Japan). Species typical of natural fields behaved in Porto Alegre much like the woods species, even though they were more numerous; their distribution was concentrated in zone H.

The drying and warming of the urban environment makes the habitats of green areas similar to the xerothermic ones (Schweiger, 1953; Trojan, 1981) favoring species which tolerate low humidity and sublight (Kouch & Sollmann, 1977; Pisarski & Czechowski, 1978). Many forest species show a preference for rather low temperatures, high humidity and shade. On the contrary the field species prefer high temperatures, low humidity and sunlight (Tischler, 1965). Naturally, the ecology of a butterfly species in the city and its success in adapting to this new environment are directly related to its ecology in natural conditions. Thus the lepidopteran species typical of fields would be better pre-adapted to urban life than forest species.

If cities are considered as well illuminated open areas, warm and with low humidity, it would be reasonable that field species would be dominant in central areas of Porto Alegre; instead, they are lacking there, since natural fields are not present. The predominant physiognomy of urban habitat is closer to a savanna, with open areas where a low vegetation can grow (in general subjected to some form of management), consisting of shrubs and trees interspersed by built-up areas. From this fundamental character of the urban habitat probably comes the predominance in urban Porto Alegre of species that are not typical either of fields or woods but prefer open areas. They are eurytopic in the sense that the adults may be observed either in grasslands or in woods or mixed areas. In the larval stage they utilize native and exotic plants widely spread over the town. The available adult and larval food apparently is the main biotic ecological factor that explain the great abundance of the dominant butterflies in the urban area of Porto Alegre (Ruszczyk, 1986). Typical of these species is their degree of vagility, which certainly has contributed to their wide distribution in the city.

## The Abundance of Butterflies in the Urbanization Zones

Figure 11 shows the number of butterflies recorded in the three samples of the urban area of Porto Alegre. All samples reveal a progressive reduction of the number of individuals in the direction of zone B. The mean number found for zone B was about 40 individuals. compared with about 64 in zone HB and about 130 in zone H. There is thus an increase of 60% from zone H to zone HB and more than 100% going from zone HB to H. This last increase already appeared in the OPs of zone HB located on the border of zone H (Figure 11d). The border between zone H and zone HB acts as a barrier for several butterfly species, especially those characteristic of field and wood environments. This border is the main transition area of the butterfly fauna in going out from the central area of the city. Its presence was obvious on the maps showing the number of individuals sampled in summer, winter and total seen as well as on diversity maps (in prep.). This border is also important for some bird species that are sensitive to urbanization (Ruszczyk et al., 1987).

The relative influence of the variable plant cover, distance from the city center and mean altitude of the OPs was analyzed for the total number of butterflies recorded, through simple correlation and multiple regression methods. The three variables showed positive correlations with the total number of butterflies, with the respective coefficients being 0.714, 0.710 and 0.456 (all significant to the 1% level). Standardization of variables gave a standard regression coefficient of 0.326 for plant cover, 0.433 for distance from the city center and 0.154 for mean altitude, all significant to the 1% level. This indicates that the

distance from the city center has a greater influence on the number of individuals than the plant cover or mean altitude. These three variables together were responsible for 61% of the explained variance of the total number of recorded butterflies for each OP. Decomposing this proportion shows the contribution of each variable:

Proportion of variance explained by all three variables	Increment due to the distance from the center of	Increment due to plant cover	Increment due to average altitude	Not attributed to either $X_1, X_2$ or $X_3$ alone
$(R^2) \\ 0.610$	the city $(\ln km)$ $(X_1)$ $= 0.092$	(arc sine $\sqrt{\%}$ ) ( $X_2$ ) + 0.041	(m) (X <sub>3</sub> ) +0.017	+0.460

Three quarters of the explained variance in the recorded number of butterflies is due to secondary effects between variables. The predominance of the single variable distance over plant cover and altitude is probably related to the large number of other variables which are directly related to it and are important to the butterflies. Variables such as temperature of the urban area, percent plant cover, degree of habitat disturbance (movement of vehicles and human beings), human population density, air pollution and intensity of urbanization are all organized as predominantly radial gradients due to the fundamental radial character of Porto Alegre's urbanization. In this way the intensity of action of these and other variables (which may be called all together anthropogenic pressure (Trojan, 1981)) on the lepidopterans depends in great portion on their position relative to the center of the city. This suggests a predominance of effects of physical factors on the distribution of these insects in urban areas (but see Ruszczyk, 1986 for a discussion of biotic factors in one common species, Papilio scamander).

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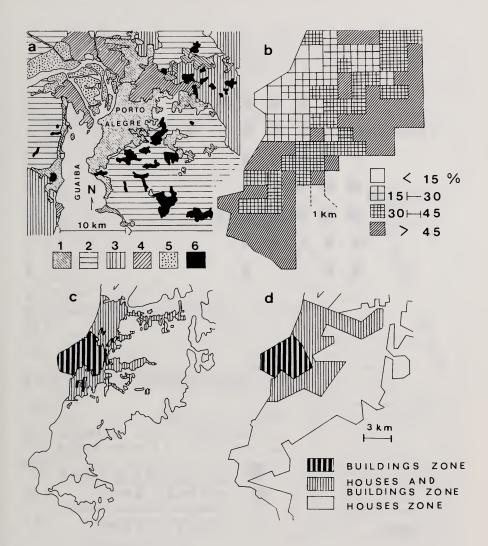


Figure 1. a) Schematic map of ecosystems within and around the city of Porto Alegre.

- 1. urban area; 2. agriculture; 3. agriculture and livestock; 4. agriculture and second growth; 5. marshes; 6. subtropical forest.
- b) Map of percent plant cover of PA.
- c) Map of urbanization zones of the city (1978).
- d) Simplification of map "c".

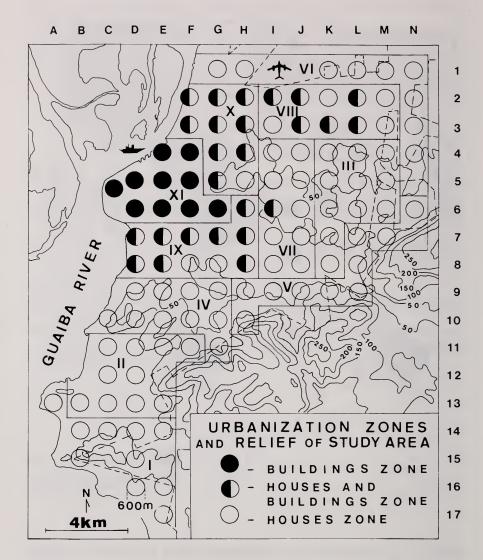


Figure 2. Location of the 111 observation points of the butterfly fauna of the city of Porto Alegre. Each observation point has a diameter of 600 m and its area was sampled three times for butterflies. The dashed line corresponds to the simplified limit of the urban area. Solid lines demarcate 11 regions into which the observation points were grouped for analysis.

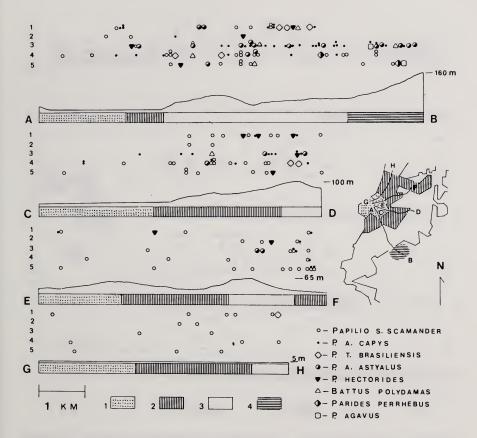


Figure 3. Family Papilionidae — Distribution in the urbanization zones of Porto Alegre. Five transects center-periphery-center (1, 2, 3, 4, 5) were made on each route in April and May 1980, February, April and May 1981, respectively. The line under the symbols is the topographic profile of the routes. The urbanization zones crossed by the routes (see map at lower right) are indicated under the topographic profile.

1. buildings zone; 2. houses and buildings zone; 3. houses zone;

4. houses zone with remnants of subtropical forest.

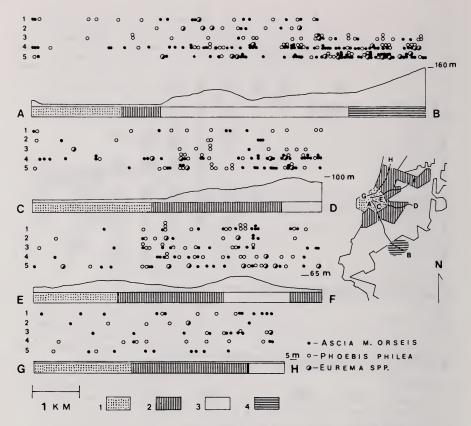


Figure 4. Family Pieridae — Distribution in the urbanization zones of Porto Alegre. See legend of Figure 3.

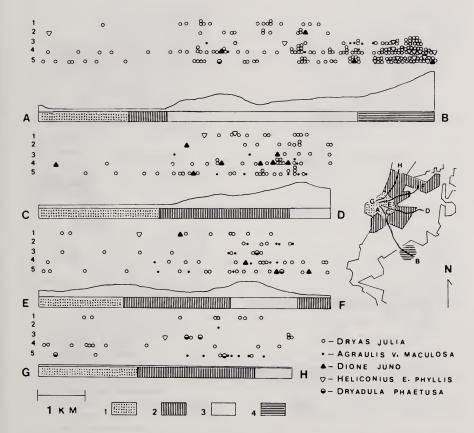


Figure 5. Family Nymphalidae (Heliconiini) — Distribution in the urbanization zones of Porto Alegre. See legend of Figure 3.

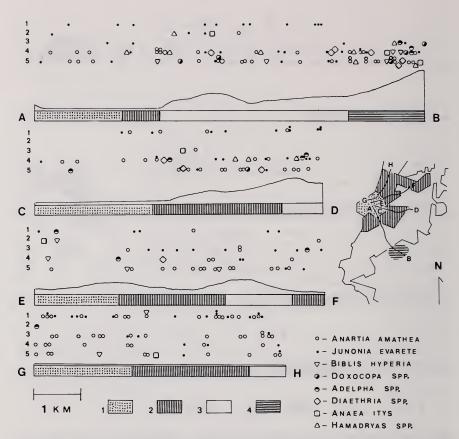


Figure 6. Family Nymphalidae (Miscellanea) — Distribution in the urbanization zones of Porto Alegre. See legend of Figure 3.

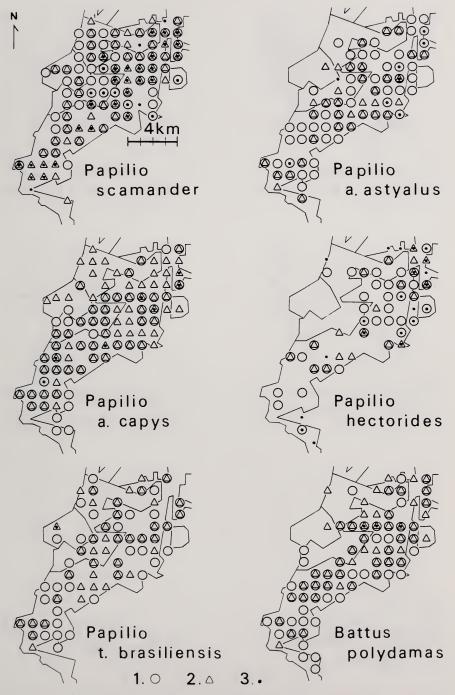
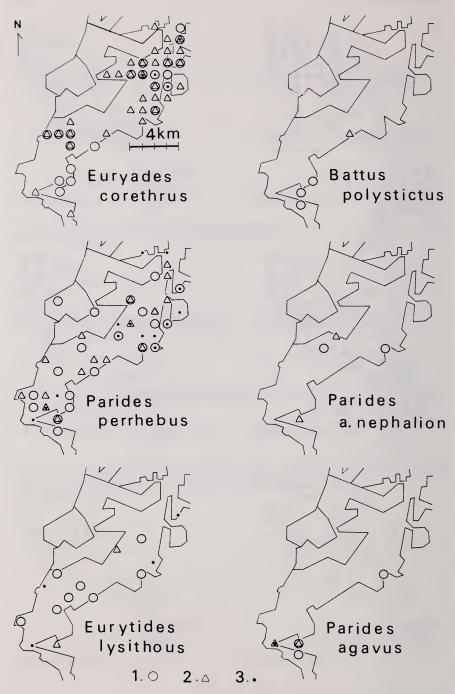


Figure 7. Family Papilionidae — Distribution in the urbanization zones of Porto Alegre. The butterfly fauna of 111 observation points of the urban area was sampled three times, in November-December 1980, March-April 1981 and June-July 1981, respectively 1, 2 and 3.



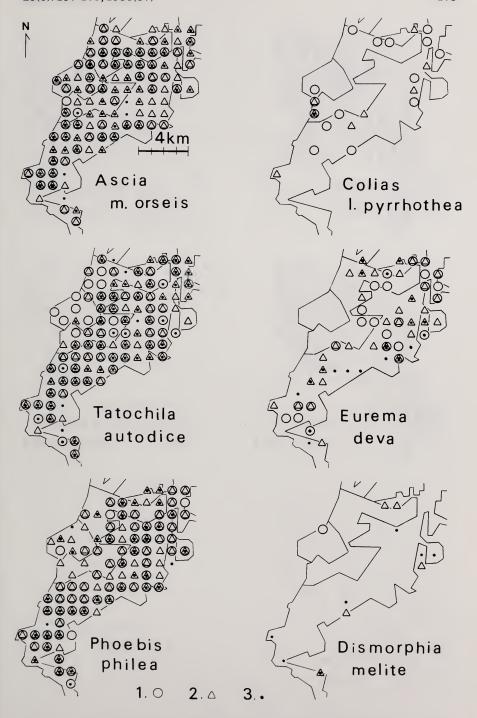


Figure 8. Family Pieridae — Distribution in the urbanization zones of Porto Alegre. See legend of Figure 7.

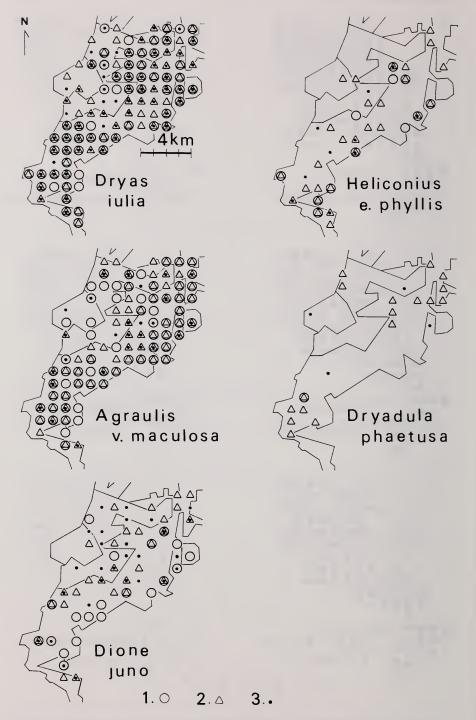


Figure 9. Family Nymphalidae (Heliconiini) — Distribution in the urbanization zones of Porto Alegre. See legend of Figure 7.

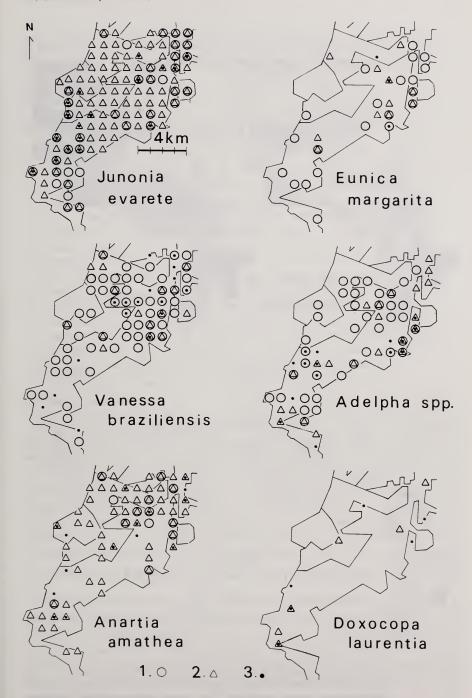


Figure 10. Family Nymphalidae (Nymphalinae) — Distribution in the urbanization zones of Porto Alegre. See legend of Figure 7.

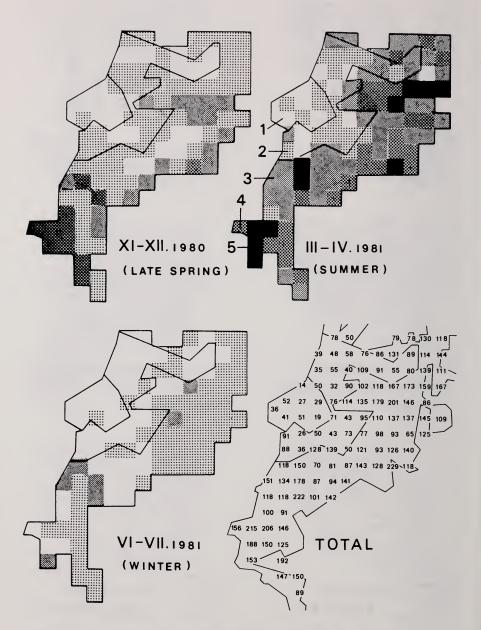


Figure 11. Number of butterflies registered during three samples in 111 observation points of the urban area of Porto Alegre. In each observation point a period of 45 min was spent walking an urban area of 600 m in diameter and recording the butterflies seen. 1, 0–16 individuals; 2, 17–40; 3, 41–70; 4, 71–100; 5, 101–135.

# The Effect of Temperature on Expression of the Dark Phenotype in Female *Papilio glaucus* (Papilionidae)

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Abstract. Experimental broods of *Papilio glaucus* produced unusual dark morph females when reared at high temperatures. Exposure to temperatures of 25–28 C during the larval and pupal stages produced adult females which were phenotypically intermediate between the normal yellow and dark morphs of the butterfly, *i.e.*, with a dusting of yellow scales in the dark background. Naturally-occurring females with this intermediate coloration have been recorded from throughout the eastern United States, but are generally infrequent. The dark morph of *Papilio glaucus* appears to be canalized (buffered) against environmental modification under natural conditions. It is proposed that canalization of the dark morph is adaptive because it protects the mimetic resemblance of dark females to the unpalatable *Battus philenor*, and that canalization is strongest in populations of *P. glaucus* from areas where *B. philenor* is an abundant model.

## Introduction

Phenotypic plasticity and polyphenism (Shapiro, 1976) in butterflies are presumably adaptive responses to heterogeneous or seasonal environments. However, developmental canalization (inflexibility of the normal phenotype over a range of environmental conditions due to the action of the epigenetic system; Waddington, 1957) is also adaptive (Shapiro, 1981; Hoffman, 1982). Phenotypic stability may be particularly advantageous in mimetic species, because environmental modification of the wing pattern would decrease the mimetic resemblance. This paper summarizes an investigation into phenotypic plasticity and canalization in the mimetic eastern tiger swallowtail, *Papilio glaucus* L.

Two subspecies of the tiger swallowtail, *P. g. glaucus* L. and *P. g. australis* Maynard, exhibit a female sex-limited wing color dimorphism (The dimorphism does not occur in *P. g. canadensis* Rothschild & Jordan). One female form resembles the male in having the typical pattern of a black-banded yellow background; the other female form is heavily melanized, with the banding pattern virtually obscured by dark scales. The dark female morph is thought to mimic the unpalatable *Battus philenor* (L.) (*e.g.*, Brower, 1958), and while both dark and yellow female morphs occur throughout the eastern U. S., the dark form is more frequent where *Battus philenor* is abundant (Brower and Brower, 1962).

Clarke and Sheppard (1957, 1959, 1962) and Clarke et. al. (1976) have provided compelling evidence that melanism in Papilio glaucus is controlled by a female-limited gene, presumably associated with the Y (W) chromosome. This is supported by the absence of the melanic form in males, and the fact that in virtually all cases, females produce daughters of the same color morph as themselves. Rare exceptions do occur in which both yellow and dark female progeny arise from a single mother (e.g., Edwards, 1884; Weed, 1917; Clarke and Sheppard, 1959). Classically, these mixed broods have been regarded as the result of abnormalities in chromosome architecture or meiotic processes, but a novel explanation for certain cases was suggested by Scriber and Ritland (in press). These authors described a genetic component in the monomorphic subspecies P. glaucus canadensis that completely suppresses phenotypic expression of the dark morph in hybrid offspring from laboratory crosses between male P. g. canadensis and dark morph female P. g. glaucus. Scriber and Ritland argued that in some cases, anomalous dark morph inheritance patterns may be the result of natural hybridization between P. g. glaucus and P. g. canadensis. The rare occurrence of analogous mutant alleles in P. g. glaucus and P. g. australis may explain other cases of unusual inheritance.

Occasionally, Papilio glaucus females exhibit wing patterns intermediate between the normal yellow and dark morphs (i.e., with a dusting of yellow scales in the dark background). The occurrence of vellow-dark intermediate individuals is an entirely separate phenomenon from the mixed broods described above. The intermediate female phenotypes are poor mimics of Battus philenor; Clarke and Sheppard (1959) postulated the presence of an efficient genetic "switch mechanism" in P. glaucus (presumably a single gene controlling melanization) which prevents the occurrence of these nonmimetic intermediates. Intermediate females of P. glaucus with significant yellow suffusion of the dark background are uncommon, but have been recorded from many areas in the eastern United States: New York (Edwards, 1884; Shapiro and Shapiro, 1973); New Jersey (Clarke and Clarke, 1983); Ohio (M. H. Evans, pers. comm.); West Virginia (Edwards, 1884); Virginia (Clark and Clark, 1951); Maryland (Clark and Clark, 1932); Pennsylvania (Shapiro, 1966; Ehle, 1981); Wisconsin (pers. obs); Mississippi (B. Mather, pers. comm.); Kentucky (pers. obs.); Georgia (Harris, 1972); and Florida (pers. obs.). Dark morph females with at least a slight suffusion of yellow scales probably occur in low frequency throughout the eastern United States.

The general rarity of intermediate females in wild populations suggests that the dark mimetic phenotype of *P. glaucus* is strongly canalized (buffered) under normal environmental conditions. Intermediate females may arise because of either *genetic shock* (e.g., mutant alleles or incomplete penetrance/expressivity of normal alleles controlling melanization) or *environmental shock* (disruption of the

canalized developmental pathway by unusual environmental conditions). The present study investigates phenotypic plasticity in dark morph *Papilio glaucus* females as a function of one environmental variable, temperature. Phenotypic plasticity and canalization of the dark morph are discussed in relation to mimicry in this butterfly. I hypothesize that canalization of the dark morph is adaptive because it stabilizes the mimetic resemblance to *Battus philenor*, and that phenotypic stability may be more strongly selected for in areas where *B. philenor* is an abundant model.

## **Methods**

Experiments conducted in 1981, 1983 and 1984 investigated the effect of rearing temperature on wing coloration in samples of *Papilio glaucus* from eight geographic areas: Dane County, WI; Dauphin County, PA; Adams County, OH; Mercer County, WV; Bell County, KY; Jefferson County, AL; Oconee County, GA; and Alachua County, FL. Laboratory cultures were established and ova for the study were obtained from dark morph females which had been mated to male siblings by the hand-pairing method of Clarke and Sheppard (1956). Females oviposited on foodplant leaves in plastic shoeboxes warmed by incandescent lights.

Newly-eclosed larvae were transferred to environmental chambers and reared at one of three constant temperatures: 22, 25, or 28 C. Temperature readings taken at different locations within each chamber indicated fluctuations of less than 0.5 C. All treatments were maintained at a photoperiod of 16L:8D to inhibit diapause and to remove photoperiodic variability as a relevant factor. The larvae were fed leaves on excised twigs of Black Cherry, *Prunus serotina* Ehrh. Foodplant turgidity was maintained by placing the twigs in Aquapics. Pupae were kept in individual screen cages at the larval rearing temperature.

All female progeny from this experiment were expected to exhibit the normal dark morph phenotype. To describe deviation from the normal dark pattern, the dorsal background color of each reared female was scored relative to a group of five reference specimens. These reference specimens represent five points on a continuum ranging from a normal dark morph female (assigned a rating of 'O') to an intermediate yellow-dark phenotype (rating = 4) which has a heavy suffusion of yellow dusting in the dark background, giving the butterfly a 'sooty' appearance (Figure 1). Reared females were compared to this reference group and assigned an appropriate score. The rating scale ranged by half steps from 0 to 4.

The modification of the dark morph pattern at different rearing temperatures was investigated statistically via the Kruskal-Wallis one-way ANOVA for ordinal data (Siegel, 1956). This procedure com-



Figure 1. Reference specimens of *Papilio glaucus* showing grading scale used to quantify dorsal wing color of experimental specimens.

pared median color rating among the three rearing temperatures within each geographic sample.

# Results

A total of 281 dark morph females from the eight geographic samples were scored for dorsal wing background color. Table 1 presents the median color ratings and range of individual scores for each geographic sample at three rearing temperatures and the associated statistics. These data indicate that higher color ratings (greater suffusion of yellow scales in the dark background) occurred under high rearing temperature regimes; *i.e.*, there was significant modification of dark morph expression at 28 C relative to the two lower temperatures. In addition, the eight geographic samples differ significantly from one another in the degree of phenotypic modification at 28 C (Kruskal-Wallis ANOVA, H = 9.4, p < .01).

Intrasample variability is relatively high at 28 C: most samples reared at this temperature contained individuals ranging over at least two full steps on the color scale (Table 1). Such individual variation in susceptibility to environmental modification (or canalization of the normal dark color pattern) may represent individual differences in the suite of modifier genes which protects the normal phenotype (Waddington, 1961). Wing pattern elements other than the melanic background (e.g.,

Table 1. Median color scores and range of individual values for eight samples of dark female *Papilio glaucus* reared at three constant temperatures. Kruskal-Wallis test statistic (H) and significance level for differences in color rating among the three temperatures are indicated for each sample.

	22 C	25 C	28 C		
Sample	median (range)	median (range)	median (range)	Н	Р
Wİ	0.0 (0.0-0.0)	0.0 (0.0-0.5)	3.0 (1.0-4.0)	16.5	.001
ОН	0.0 (0.0 - 0.0)	0.0 (0.0-2.0)	0.5 (0.0 - 3.5)	8.9	.05
PA	0.0 (0.0-0.0)	0.0 (0.0-0.0)	1.8 (0.0-2.5)	21.4	.001
AL	0.0 (0.0-0.0)	0.0 (0.0-0.0)	0.8 (0.0-1.0)	11.5	.01
WV	0.0 (0.0-0.0)	0.0 (0.0-0.0)	0.3 (0.0-2.5)	4.4	.20 (N.S.)
KY	0.0 (0.0 - 0.0)	0.5 (0.0-2.0)	2.0 (1.0-2.5)	8.8	.05
GA	0.0 (0.0-0.0)	0.3 (0.0-0.5)	0.5 (0.0 - 3.5)	12.5	.01
FL	0.0 (0.0-0.0)	0.0 (0.0-1.0)	0.0 (0.0-3.0)	12.1	.01

the "tiger" stripes and wing margin borders) were virtually unaffected by temperature. The yellow forewing discal spot present in some females (see Figure 1) becomes more pronounced at higher rearing temperatures (Ritland, 1983), but varies independently of melanic background color in individual butterflies.

## Discussion

Constant rearing temperatures of 25 and 28 C destabilized the dark morph phenotype of Papilio g. glaucus and P. g. australis. A previous experiment (Ritland, 1983) suggested that pattern development is susceptible to temperature modification only during the pupal stage; this is consistent with the suggestion (Clarke and Clarke, 1983) that the melanic background pattern develops just before adult eclosion. The physiological basis of aberrant intermediate pattern development is not known, but many processes involved in wing pattern development (including pigment synthesis, wing scale maturation, and hormonal control systems) are subject to modification by temperature (Goldschmidt, 1938; Hintze-Podufal, 1977; Nijhout, 1980). The temperature sensitivity of tyrosinase-mediated melanization processes in particular is well known (Waddington, 1961; Fuzeau-Braesch, 1972; Majerus, 1981), and high rearing temperatures may also disrupt the pteridine pigment system involved in P. glaucus pattern development (Oldrovd, 1971).

Aberrant intermediate phenotypes were expressed only in individuals reared at 25 C and above, suggesting the existence of a temperature threshold above which canalization of the normal dark phenotype breaks down. Developmental pathways are protected by such genetically-determined thresholds (Waddington, 1961), thereby canalizing the normal phenotype over a wide range of natural conditions.

This experiment did not investigate photoperiodic effects on pattern modification in *Papilio glaucus*, but photoperiod is potentially relevant

in the field. Long and short photoperiods induce different seasonal forms and aberrations in many butterfly species (*e.g.*, Ae, 1957; Pease, 1962; Fukuda and Endo, 1966; Shapiro, 1976; but *cf.* McLeod, 1968 and Lewis, 1985 *re* species which are insensitive to photoperiodic manipulation).

The genetic capability to produce the intermediate phenotype represents a component of the *P. glaucus* genome which is not normally expressed, probably due to a combination of the genetic switch mechanism proposed by Clarke and Sheppard (1959) and developmental canalization. While the experimental conditions of this study (24 hr thermoperiod + 16:8 photoperiod) do not represent natural conditions, the range of rearing temperatures certainly lies within natural limits. This experiment is therefore qualitatively different from "shock" studies, in which newly-formed pupae are exposed to extreme heat or cold. Such shock treatments can produce striking pattern modifications, but also kill or cripple the majority of individuals, suggesting that critical developmental pathways are disrupted. Changes in wing pattern induced by such radical conditions may be of questionable ecological relevance. In sharp contrast to shock studies, the relatively mild conditions of the present investigation produced aberrant wing patterns but did not significantly reduce survival or adult viability (no significant difference in viability among the three temperature regimes; chi-square p < .01). It is significant that such moderate experimental conditions could produce such extreme phenotypic modification, given the fact that intermediates are so uncommon in the wild. This intriguing situation is similar to that described by McLeod (1968), who found that the African nymphalid Precis octavia, which exhibits discrete seasonal forms in nature, produced a wide variety of intermediate forms in his laboratory temperature studies.

Environmental modification of wing pattern may disrupt mimicry in dark morph *Papilio glaucus* females; the intermediate phenotypes produced at 25 and 28 C appear to be very poor mimics of *Battus philenor*. The eight geographic samples in this study differed significantly in expression of the intermediate phenotype at 28 C (Table 1). Both the proportion of aberrant individuals and the degree of phenotypic alteration varied between samples. Samples from the periphery of the dark morph range, where *Battus philenor* is uncommon (*e.g.*, Wisconsin and Pennsylvania) were relatively susceptible to temperature modification (as indicated by the high median color ratings at 28 C). In contrast, samples from areas where *B. philenor* is abundant (West Virginia, Georgia, Alabama, north Florida) seemed to be more strongly canalized (buffered) against environmental modification. The West Virginia sample, in fact, showed no evidence of phenotypic modification by temperature.

These results are consistent with the hypothesis that canalization of the dark morph is adaptive because it stabilizes the mimetic color pattern, and that the dark phenotype is most strongly canalized in areas where it confers the greatest mimetic advantage, *i.e.*, where *Battus philenor* is abundant as a model. In regions where *B. philenor* is rare and is therefore not an effective model, the selective advantage of the dark morph relative to the yellow morph is decreased; selection for genetic modifiers which canalize the dark morph developmental pathway should also be reduced. It is significant that many of the records for wild intermediates occur near the periphery of the dark morph range, where *B. philenor* is rare.

The occasional occurrence of wild intermediates of P. glaucus may be due to either environmental influences (environmental shock) or direct genetic control (genetic shock). Microhabitat selection by pupating larvae (e.g., West and Hazel, 1979) may occasionally result in exposure to high temperatures which disrupt the normal dark morph developmental pathway and cause expression of the intermediate phenotype. Alternatively, mutant alleles may alter the canalization threshold of the normal dark morph (i.e., change the developmental pathway), such that the intermediate phenotype is expressed under normal environmental conditions. Such alleles might be related to the gene(s) in P. glaucus canadensis that inhibit expression of the normal dark morph (Scriber and Ritland, in press). Similar inhibitory genes have been described in Papilio rutulus; hybrid crosses between male P. rutulus and dark morph female P. glaucus produce intermediate daughters (Clarke and Willig, 1977) that resemble the environmentally-produced intermediates (phenocopies) described in this study.

The interaction of genetic and environmental factors affecting pattern development in *Papilio glaucus* may significantly alter the resemblance to *Battus philenor*. The data presented in this paper support the hypothesis that canalization of the dark female morph stabilizes the mimetic color pattern under normal environmental conditions, and that geographic variation in the degree of phenotypic canalization is correlated with the abundance of *Battus* philenor.

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# Chromatic Polymorphism in *Callophrys mossii bayensis* Larvae (Lycaenidae): Spectral Characterization, Short-Term Color Shifts, and Natural Morph Frequencies

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Abstract. A tristimulus colorimeter and UV-VIS spectrophotometer supplemented visual assessments of color polymorphism in wild fourth instar larvae of the endangered butterfly *Callophrys mossii bayensis*. Wild larvae are of many color hues; this contrasts with the distinct morphs reported from laboratory rearings. Larval color changed over short time periods when fed yellow flowers or red bracts. The preciseness of visual color matching between larvae and plant substrates is higher for red than for yellow larvae. This crypsis does not extend to any precise mimicry of spectral reflectance. Genetic color-determining mechanisms seem to be supplemented by an environment-derived factor in producing the broad range in color hues found in wild larvae. The color-assessment techniques described here could be used to better understand the role of color pattern in thermoregulation, sexual selection and predation-avoidance.

#### Introduction

Body color is a universal life attribute that influences intraspecific communication, predator avoidance, and/or thermoregulation. Systematists use color patterns to characterize species and subspecies, especially in avian and lepidopteran taxa. Despite these important roles, color patterns are usually qualitatively described, not quantitatively characterized. Partly, this is due to the difficulty in quantifying and standardizing color description. Color standard texts (e.g., Munsell, 1963) are useful, but not widely accessible. Each text uses different descriptors and their value is limited mainly to mono-colored organisms.

An added complexity is the variation in color pattern within populations. This is particularly apparent in the Lepidoptera, with color polymorphism occurring in LARVAE (e.g., Poulton, 1888; Bell & Scott, 1937; Pinhey, 1960; Clarke, Dickson & Sheppard, 1963; Curio, 1965,

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1970a, 1970b, 1970c; Boer, 1971; Emmel & Emmel, 1973; Common & Waterhouse, 1981; see also Edmunds, 1974), PUPAE (Poulton, 1890; Sims & Shapiro, 1983, and citations therein), and ADULTS (Ford, 1955; Kettlewell, 1961; Clarke & Sheppard, 1963, 1972; Owen & Chanter, 1969; and citations in Wickler, 1968 and Rettenmeyer, 1970). Larvae of the federally endangered (U.S. Fish & Wildlife Service, 1976) San Bruno elfin butterfly, *Callophrys mossii bayensis* R. W. Brown exhibit a striking color polymorphism, with chromatic variability of both larvae and foodplant substrates. This provides an ideal situation for comparing color assessment techniques.

# Callophyrs mossii bayensis Color Morphs

Brown (1969) first described color morphs in third and fourth instar C. m. bayensis. He felt that greenish, fresh-hatched larvae acquired the same color as the Sedum spathulifolium Hooker foodplant part they ingested. Sedum exhibits diverse colors in late spring when larvae are near maturity: Basal leaf rosettes range from deep green to rosy red. Flowering stalk stems and bracts are initially green, becoming pale to rosy, or deep red; petals are yellow.

Brown's assessment of color determination was disputed by Emmel and Ferris (1972), who described three distinct color morphs from laboratory-reared fourth instars fed only green *Sedum* rosettes: yellow, pale orange, and cherry red. Arnold (1978, 1983), in turn, disputed the concept of three distinct morphs: "Newly eclosed larvae were colored either red or yellow. They remained one color throughout their larval life," and "larvae possess two distinct color morphs, red and yellow, plus an intermediate light orange." Lumping light orange and yellow larvae, Arnold proposed a simple 1:3 allelic expression of yellow:red forms, and equated laboratory and field expression of larval color. Finally, our repeated field observations of an array of color forms conflicts with all previous reports of two or three distinct morphs in nature. Clearly, there are discrepancies regarding the expression of color, its stability, and its derivation in *C. m. bayensis*. This paper seeks to resolve some of them.

# **Materials and Methods**

C. m. bayensis and Sedum spathulifolium samples were obtained on north-facing slopes of San Bruno Mountain (San Mateo County) California between Brisbane and Colma Canyon. Larvae occur from about mid-March to very early June. About mid-May, third and fourth instar larvae ascend to budding Sedum flower stalks (Emmel & Ferris, 1972; Arnold, 1983). We took food-plant and fourth (penultimate) instar samples after ascent.

COLOR CLASSIFICATION SCHEME: Following a preliminary 1977 field examination, a scheme was developed to quickly color-sort wild larvae: Seven larval "standards" (Fig. 1) divided the visual color range of

wild larvae. These were sequentially numbered; the higher the number, the more red (or less yellow) the larva. These were photographed with Kodachrome 25 film, using two Sunpak 411 flashes. Subsequent Kodak color prints facilitated rapid color classification in the field. Although film color reproduction is inexact, we found no problem placing wild larvae into one of seven color categories. A "color category" represents a range between two points defined by the larval standards, except for Category 7 which had only one larval standard "anchor." A larva whose general color fell anywhere between the discrete point of Standard 1 up to, but not matching Standard 2, was a Category 1 larva and so on. COLORIMETER ANALYSIS: Live larval and foodplant samples were color-analyzed using a Hunterlab Tristimulus Colorimeter Model D25M-9. This employs a source-photodetector-filter combination to simulate the colormatching response functions of a "normal" human observer. Quantifiable, repeatable results are in the form of the L<sub>1</sub> a<sub>1</sub> b<sub>1</sub> (henceforth, LAB) system (Hunter, 1975). "L" measures brightness (L = 100 for pure white, 0 for pure black). "A" and "B" are chromaticity dimensions. The value of "A" indicates redness (+ value), gray (0 value), and green (- value). "B" measures yellowness (+ value), gray (0 value) and blue (- value). Measurements were made by holding similar-sized samples of Sedum flowers and adjacent bracts, secondary bracts, green rosettes, or C. m. bayensis penultimate instar larvae against the 1/2-inch diameter port.

SPECTRAL ANALYSIS: A Cary UV-VIS spectrophotometer with spectral capacity of 187–875 nanometers (nm), and equipped with a diffuse reflectance sphere, was used. Larval and foodplant samples were affixed in similar orientation on coal black cards with double-stick tape. Each sample was scanned at 1 nm/second, with a spectral band width of 3.5 nm, allowing resolution of narrow reflectance peaks. To reduce sample orientation effects, all samples were positioned similarly. After scanning, larvae were released unharmed by wetting the double-stick tape. LARVAL COLOR CHANGES: To explore short-term color changes, fourth instar larvae with previous access to all *Sedum* plant parts were segregated into color categories using the seven standards. Free access to all foodplant parts was maintained under low intensity fluorescent lighting. Forty-eight hours later, the larvae were color-reclassified. Only tachinid parasitoid-free larvae (assayed at pupation) were used in the data analysis.

We investigated Brown's (1969) statement that larval and ingested food colors converged: Larvae that had ingested only green rosettes for two days were grouped into pairs of identically colored larvae and color-classified. For the following 48 hours, one member of each pair was provided only yellow Sedum flowers; the other was given only very red flower stalk bracts. All experienced the same fluorescent light exposure. Pairs then were reunited and color-compared, using the larval standards. Only parasitoid-free larvae were used in the data analysis.



Fig. 1. Seven larval "standards" used to characterize color polymorphism in wild *Callophrys mossii bayensis*. Standards are labeled sequentially, starting with the most yellow (Top row, 1–4; bottom row, 5–7).

Fig. 7. (LEFT BELOW) Larval color shift from light to dark over a 48-hour period. LEFT: Flower-fed larva now in color Category 3, formerly Category 2; RIGHT: Red bract-fed larva, unchanged in Category 2.

Fig. 8. (RIGHT BELOW) Larval color shift from dark to light over a 48-hour period. LEFT: Flower-fed larva now in color Category 5, formerly Category 6; RIGHT: Red bract-fed larva unchanged in Category 6.



#### Results

QUALITATIVE DESCRIPTION OF LARVAL COLOR: Nearly 500 wild larvae were color-classified. Virtually none were lighter yellow than Standard 1; some had less pronounced "chevrons," the paired, dorso-lateral curved markings occurring on many body segments. Category 7 proved exceptionally restrictive, since few Category 7 larvae were redder than Standard 7.

Larvae within each color category can be generalized as follows:

- 1 = Yellow, no peach tint; chevron markings generally faint
- 2 = Yellowish with faint orange tint; distinct chevrons.
- 3 = Distinctly light orange with slightly darker rosy suffusions; chevrons usually with pale outlines.
- 4 = Orange with darker peach-colored suffusions on much of the body; chevron outlines and dorsal midline generally pale.
- 5 = Orange with brownish tinge; dark chevrons and less distinct pale outlines.
- 6 = Rosy red, with less distinct but noticeable pale chevron outlines. Larvae in this category may be lighter colored than the previous category, but are distinctly redder.
- 7 = Cherry red throughout; chevrons generally faint.

While color category designation was based upon general background color, ignoring fine-scale pattern differences, we also noted that chevron markings did not intensify in direct relation to increasingly red background coloration (see Emmel & Ferris, 1972).

COLOR DISTRIBUTION IN NATURE: Fig. 2 shows the color distribution of 433 wild larvae, comparing the results to distributions obtained by Emmel and Ferris (1972) for wild larvae, and Arnold (1978) for laboratory-rearings. This alignment easily satisfied the "morph" descriptors provided by each author for his respective sample. Our categories 2 and 3 are the only ones that would fit the definition of "light orange" (sensu Arnold, 1978).

Our sample indicates larvae to be broadly distributed across color categories, at these frequencies: 1=6.0%; 2=10.6%; 3=14.6%; 4=13.9%; 5=12.0%; 6=24.7%; 7=18.3%. Further, our sample yielded lower frequencies of "pure" yellow (Category 1) and red (Category 7 and possibly 6) larvae than reported for laboratory rearings. Conversely, greater frequencies of "intermediate" colors were found. Even when restricting "intermediates" to larvae of categories 2-3, our combined frequencies of yellow plus "light orange" larvae (over 30%) exceed that of the laboratory-reared sample (24.4%; Arnold, 1978). Unfortunately, Arnold did not segregate frequencies for yellow and light orange larvae. Yet, he states that only "a few individuals are light orange" (Arnold, 1983), which tends to corroborate our observations of rosette-reared larvae, and by deduction, confirms the much rarer occurrence of "pure yellow" larvae in nature.

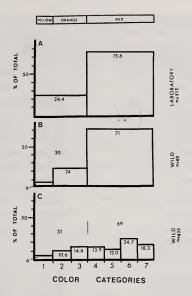


Fig. 2. Color category distribution of *C. m. bayensis* larvae: Comparisons of wild- and laboratory-derived samples, from (A) Arnold, 1978; (B) Emmel & Ferris, 1972; (C) this study. Alignments are based upon each author's color descriptions of cited morphs. Frequency figures within each bar pertain to that study. Above-bar frequencies in (B) and (C) are provided to facilitate cross-sample comparisons.

COLORIMETER VALUE COMPARISONS: Table 1 lists LAB values for *C. m. bayensis* larval standards and foodplant samples. Predictably, "A" values are higher for the "redder" larval standards, although the most yellow standard reflects some red. The "redness" increase, measured by "A," changes little for standards 2–5, increasing for 6 and 7. In contrast, "yellowness," measured by "B," drops in significant increments through standard 5. Thus, while larval standards broadly cover the yellow-to-red spectrum, they do not represent evenly spaced color points for either chromaticity dimension. This is clear in the composite expression of color (subtracting "A" from "B" for each sample; Table 1). These findings, however, again confirm a graded expression of color in wild larvae within their spectral range.

The range in larval LAB values approximates that of foodplant parts (Table 1). However, pale or yellowish flowering stalk substrates (flowers+associated racemes) exhibit significant green colorimeter values (i.e., negative "A") that are not duplicated in any larval standards or in Category 1 larvae. In contrast, there is close matching of "A" and "B" values for the reddest Sedum samples and larvae.

SPECTRAL VALUE COMPARISONS: Sample orientation (Fig. 3), brightness, and other features of the sample can affect absolute reflectance values. However, basic reflectance peaks and dips are relatively

Table 1. LAB colorimeter values for *Callophryr mossii bayensis* larval standards and *Sedum spathulifolium* foodplant samples. Variation of each sample did not exceed 10% between readings as long as orientation positions were kept constant.

Sample			•	Color Values				
			L	Α	В	(B-A)		
Larva:	Color Sta	andard 1	37.52	2.81	12.17	9.4		
	Color Sta	andard 2	36.51	4.01	10.21	6.2		
	Color Sta	andard 3	35.52	4.53	8.95			
	Color Sta	andard 4	35.02	4.68	6.65			
	Color Sta		34.08	4.91	4.37			
	Color Sta		34.30	6.83				
	Color Sta	andard 7	32.94	7.72	3.76	-4.0		
Sedum	Flowers:	Sample 1	35.27	1.80	24.13			
		Sample 2	40.59	3.45	15.36			
		Sample 3	45.22	-2.05	19.70	l		
		Sample 4	40.55	.70	17.33			
		Sample 5	36.73	-1.74	18.22			
Sedum	Leaves:	Sample 1	33.17	-6.03	13.01			
(green)		Sample 2	40.88	-6.82	12.42			
		Sample 3	47.21	-5.90	13.60	)		
		Sample 4	38.74	-2.85	5.59			
Sedum	Bracts:	Sample 1	33.14	9.08	3.56	5		
(reddis		Sample 2	28.23	6.27	3.55	5		
		Sample 3	35.41	4.33	4.97	1		
		Sample 4	38.10	7.44	3.34			
		Sample 5	44.20	4.97	2.19	)		
Cumulative Spectral Ranges:		L	1	4	В			
Larvae			32-37	2.8	-7.7	3.8-12.2		
Foodplant Rosettes			28-47	-6.0	-9.1	2.2-24.1		
Flowering Stalk			28-45	-2.1	-9.1	2.2-24.1		

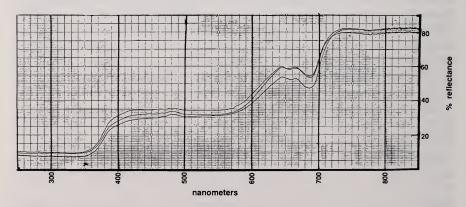


Fig. 3. Reflectance spectra of a *Sedum spathulifolium* leaf sample placed at different angles in the spectrophotometer diffuse reflectance sphere sample port.

constant. For this reason, we limited our spectrograph comparisons to reflectance curves (slopes).

In the ultraviolet and infrared (Fig. 3), no distinguishable intersample differences were found. All samples reflected strongly in the red and near-infrared range but weakly in the ultraviolet.

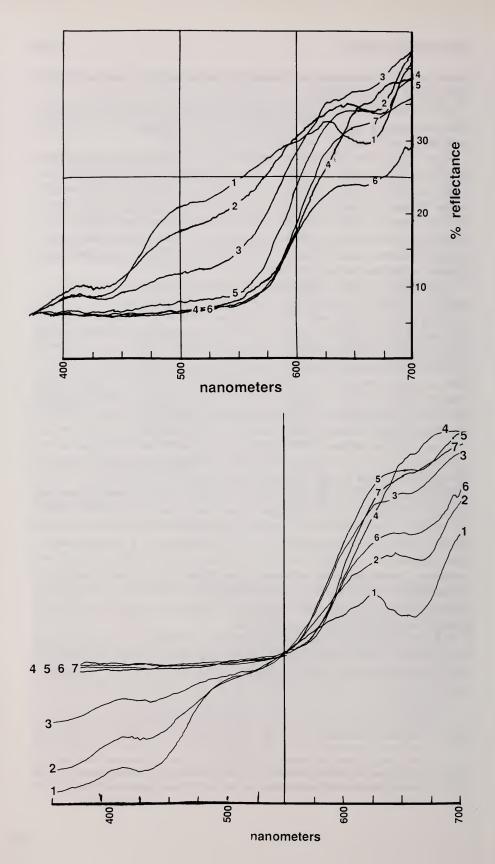
Figure 4A shows reflectance curves for the larval color standards. Predictably, Standard 1 (yellow) reflects highly between 600-630 nm, while Standard 7 (red) exhibits a sharp reflectance drop at wave-lengths under 640 nm. Reflectance differences are less pronounced for standards that are closer in visual color. In Figure 4B, the curves are aligned at 550 nm to show relative similarities. Standards 4-7 reflect almost identically below 550 nm. Standards 1-3 show similar reflectance patterns but greater variation, especially Standard 1.

Regardless of visual appearance, S. spathulifolium samples (Fig. 5) usually exhibited a broad absorbance peak (reflectance dip) at 670-680 nm. Dry flower stalk stems (Fig. 5: ST) were the only exception. Larvae that matched standards 1 and 7 were run sequentially with like-colored Sedum parts (yellow blossoms or deep red flower head bracts (Fig. 6). Visual colors are not backed by fine-scale spectral reflectance mimicry. Most conspicuously, the foodplant reflectance dip at 670-680 nm is absent. As seen in the colorimeter data, larval Standard 1 does not show the strong yellow-green reflectance peak of the Sedum flower sample. Moreover, while the slope of Standard 7 and its red Sedum counterpart are very similar between 600-630 nm, at shorter wavelengths larvae have relatively higher reflectance values. Possibly, these plant-caterpillar differences are partly derived from structural disparities.

COLOR SHIFTS IN INDIVIDUALS: Over one-third of larvae given free access to foodplant parts changed color over a two-day period (Table 2); some changed within the first day. Color shifts occurred in larvae of all color categories examined (1-5), with Category 4 a possible exception. All but one (a shift from 5 to 3) of the 16 color shifts spanned one category. As defined here, a larva "color shifts" by crossing at least one color anchor (defined by a larval standard). However, two larvae experiencing the same "one category" change, in reality, may have shifted significantly different amounts.

Table 3 summarizes color shifts of 34 color-matched pairs, after being fed different-colored *Sedum* parts. Fifteen out of 68 larvae colordiverged from their pair mates; two examples, in different spectral directions, are illustrated in figures 7 and 8. As in the previous experiment, a

Fig. 4. Reflectance spectra of *C. m. bayensis* larvae. A: Scans from "most yellow" (Standard 1) to "most red" (Standard 7) larvae in the 400–700 nm range; samples were of like size, so major differences in absolute reflectance values between samples are valid. B: Realignment of the seven larval standard scans at 550 nm show relative similarities of curves.



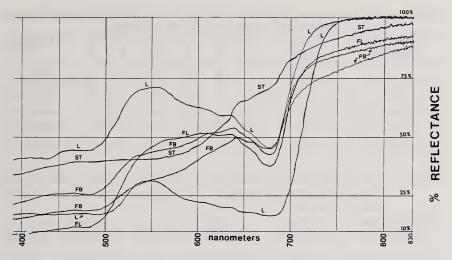


Fig. 5. Reflectance spectra of different *S. spathulifolium* foodplant parts: L = green rosette leaf; ST = dried, reddish flower stalk; F = yellow flowers; FB = yellow flowers and associated green and reddish bracts and stems.

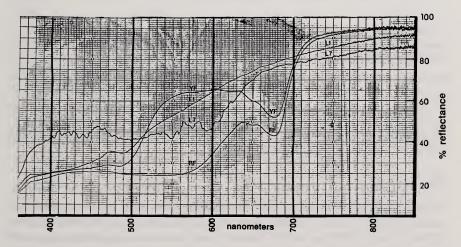


Fig. 6. Comparative reflectance spectra for similar-colored *S. spathulifolium* foodplant and *C. m. bayensis* larval samples. RED: Larva in Category 7 (L7), *Sedum* red flower stalk stem leaf (RL); YELLOW: Larva in Category 1 (L1), *Sedum* flower petals (YF).

slightly higher percentage of Category 1 and 2 "yellow" morphs experienced color shifts, in contrast to redder individuals. However, color shifts were often not in the direction of the foodplant part's color: Six larvae fed yellow flowers color-shifted towards red; only two became more yellow. In total, two-thirds of the 15 recorded color changes involved shifts towards red. As in the previous experiment, a single two-category shift was recorded (from Category 1 to 3).

Table 2.	Color changes which occurred in color category-segregated groups
	of C m havensis larvae over a 18-hour period

Original Color Category	Sample Size	#W 1			Color 4			% Change
1	10	6	4	0	0	0	0	40%
2	8	2	5	1	0	0	0	60%
3	7	0	2	3	2	0	0	57%
4	10	0	0	1	9	0	0	11%
5	10	0	0	1	2	<u>6</u>	1	40%
Totals:	45	8	11	6	13	6	1	36%

Table 3. Color divergence in color-matched pairs of *C. m. bayensis* larvae fed either yellow *Sedum* flowers or red flower stalk bracts over a 48-hour period.

Original Color	# Pairs	Bract-f	ed	Flower-fed		
Category	Tested	Color-shift	No shift	Color-shift	No shift	
1	3	1(#2) 1(#3)	1	1(#2)	2	
2	7	1(#3)	6	4(#3)	3	
3	4		4		4	
4	6		6	1(#5)	5	
5	1		1		1	
6	8	3(#5) 1(#7)	4	2(#5)	6	
7	5		5		5	

<sup>%</sup> of larvae, categories 1-2 (n=20), showing color shift: 40%

Collectively considering data from both color shift observation experiments, 11 out of the 12 possible one-category shifts are present (absent: Category 7 to 6 shift).

# Discussion

COLOR ASSESSMENT TECHNIQUES: Treating color pattern in greater detail may increase our understanding of color-related phenomena (e.g., Endler, 1978, 1984). Color assessment techniques could be employed more widely in studies of antipredation thermoregulation, sexual selection, and more broadly, in evaluating how how precisely selective pressures operate on elements of a color pattern. Colorimetric and spectrophotometric data are fairly unbiased and repeatable ways of defining color. On the negative side, acquisition of these data may be time-consuming and equipment is not always available.

The most likely application of spectrophotometer data is in assessing the fine degree of color matching between organism and substrate over the spectral absorbance range. This relates to antipredation strategies, and such information could yield useful clues on the parameters that influence prey-substrate matching: predator vision, predative pressure, and the prey's genetic constraints. Spectrographs

<sup>%</sup> of larvae, categories 3-5 (n=22), showing color shift: 5%

<sup>%</sup> of larvae, categories 6-7 (n=26), showing color shift: 23%

<sup>%</sup> of color-shifting larvae (n=15), shifting towards RED: 66% shifting towards YELLOW: 33%

might also be useful in picking out underlying genotypes in a diffuse range of phenotypes, since they magnify any subtle spectral differences.

In contrast, the colorimeter seems most ammenable to speedy color-quantification and for generally comparing intraspecific color morphs and their background substrates. Most suited are fairly monochromatic organisms and substrates whose color pattern nevertheless defies simple description. Since the colorimeter yields data that incorporate the color-matching response of the human eye, there is a possible drawback: Color-differentiating abilities of humans may be quite different from that of lizard and avian predators. Also, colorimeter information does not reflect intra-human variation in color-matching.

DUAL COLOR-INFLUENCING MECHANISMS IN *C. M. BAYENSIS*: While our larval standards technique is less sophisticated than the analytical methods, it nevertheless has demonstrated that (1) a range of color patterns exists in nature; (2) color pattern is not static; (3) color pattern can shift towards red or towards yellow; (4) both "red" and "yellow" wild larvae can change color; and (5) color shifts can occur over short time frames. Some of these results obviously counter previously published statements, but we see a possible resolution of the contradictions.

Genetic larval color determinants for *C. m. bayensis* are suggested by Emmel and Ferris (1972) and Arnold (1978, 1983). Their observations, derived from rosette-reared larvae, corroborate ours. Arnold proposed a dimorphic expression of a single allele leading to red homozygous and heterozygous dominants, plus a yellow homozygous recessive. Although no backcrosses were conducted to confirm this, the hypothesis is tenable. At the same time, it neither explains the varied color expression we describe, nor Arnold's own finding of "a few light orange" larvae. Clearly, an additional color-influencing mechanism is present.

Could the mechanism that generates light orange larvae in the laboratory also be producing intermediate colors in nature? We offer no definite answers. However, neither temperature and humidity parameters, nor developmental changes in color seem to be the driving forces. We agree with previous authors (Emmel & Ferris, 1972; Arnold, 1983) that no direct connection exists between the color of ingested plant parts and resultant larval colors. Yet, we do not preclude a less direct relationship. Indeed, the fact that laboratory-maintained larvae allowed access to all Sedum parts color-shift — while rosette-reared larvae seemingly do not — is indication that diet does have an influence on color.

Color in larval *C. m. bayensis* probably offers predation-avoidance advantages, but the specifics are unclear. Why, for example, are most full-grown larvae red, while the most frequently occupied substrate is yellow, if crypsis is the antipredator strategy? And does dual-mechanism color determination offer advantages over genetic or environmental

determinants alone? Approaching these questions from both mechanistic and ecological perspectives, using descriptive information as a foundation, may offer answers. All-told, we suggest there is greater value in exploring the subtleties of color expression in this taxon, rather than burying them.

Acknowledgements. The invaluable assistance of David Schooley is gratefully acknowledged, as well as constructive critical comments on the manuscript by Clifford Ferris and Arthur Shapiro. The Permit Branch of the Office of Endangered Species (U.S. Fish & Wildlife Service) and California Department of Fish & Game provided study permit #PRT 2–757.

We appreciate the color plate opportunities of the Journal of Research on the Lepidoptera. When a picture is worth a thousand words, color photographs are beyond value in communicating the details of this topic!

Finally, we salute the many lepidopterists, botanists, biologists, and local citizens to whom *C. m. bayensis* owed its continued existence. Aware of the uniqueness of San Bruno Mountain's habitats and native inhabitants, they have actively worked for the protection of this national resource using their diverse scientific, educational, and political talents.

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**Opinion.** Opinion is intended to promote communication between lepidopterists resulting from the content of speculative papers. Comments, viewpoints and suggestions on any issues of lepidopterology may be included. Contributions should be as concise as possible and may include data. Reference should be limited to work basic to the topic.

# Comments on Clench's Temporal Sequencing of Hesperiid Communities

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Competition for adult resources as a structuring force in butterfly communities was first suggested by Clench, (1967) who demonstrated the existence of five sets of hesperiid species at one locality in which competition was apparently minimized by several mechanisms. Within each set of species, the timing of adult flight period was such that the species replaced each other during the course of the summer (Figure 1). Peak populations of one (set 2) coincided with the minimum populations of another (set 1). Furthermore, at least two of the sets (1 and 2) seemed to utilize different heights of nectar sources. Thus, adult competition within each of these sets was minimal due to the sequencing of the species and competition between at least sets 1 and 2 was minimal.

Clench's data were generated over an 11-year period at the Carnegie Museum's Powdermill Preserve, and were primarily qualitative, including rough estimates of adult density, estimation of adult flight period, and observations of nectar use by each species. While his results are intriguing, there are problems in his assumptions which render his conclusions obsolete. Because of the frequency with which this paper is cited, especially in review articles, (e.g., Ehrlich, 1984; Gilbert and Singer, 1975; and Shapiro, 1975) which portray Clench's results as interesting if somewhat nebulous, a short discussion of this paper seems warranted.

Clench's main assumptions were simple: that adult hesperiid populations may be (or may have been in the past) limited by adult nectar resources, and that competitive interactions over limiting resources between species can structure communities. I agree wholeheartedly with him on these basic assumptions. My own data (Shuey, 1986) on wetland hesperiids indicate that resource partitioning is a possibility under certain conditions. Moreover, Pivnick and McNeil (1985) have recently established the importance of adult resources to one hesperiid species. Citing unpublished data, they reported that the availability of nectar increased the fecundity of *Thymelicus lineola* 27 times over that

of females which did not have access to nectar (availability of nectar could therefore have a dramatic selective impact if it was in limited supply).

Unfortunately, Clench also assumed that the community he studied had experienced the stable interactive history that would facilitate the evolution of resource partitioning. He restricted his study to hesperiids inhabiting moist to dry fields, communities that are artificially maintained in early successional states and often dominated by exotic species. The hesperiids studied (Figure 1) were mostly opportunistic species and hence unlikely to have experienced the type of pressures necessary to establish resource partitioning via past competition. Clench's admission that his temporally distributed species sets did not exist 200 miles east of his study site (despite the absence of any obvious barriers to gene flow for the hesperiids in question) indicates that these sets may be artifacts of other factors such as host plant phenology

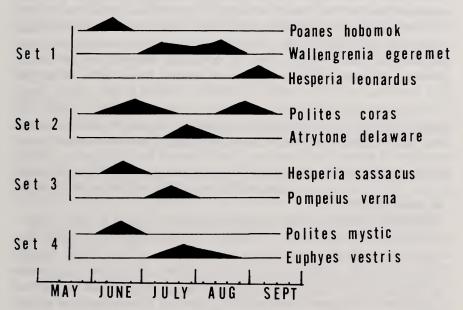


Figure 1. The average flight periods of Clench's (1967) Hesperiinae sets 1 to 4. Relevant to his arguments are the "temporal replacement of the members within each set, and the coincidence of the peaks of Set 2 with the intervals (population minima) of Set 1." The species in set 1 were the largest and most common during his study and had a "decided preference" for tall flowers. The species of set 2 generally fed on low-growing flowers but had "been observed at times on tall flowers, suggesting a certain degree of active competition with set 1 species." The remaining sets showed no cohesive nectar source preferences. A fifth set composed of *Polites themistocles* and *Polites origenes* was present but too rare for Clench to present data. (Redrawn with permission from Clench, 1967).

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(Slansky, 1974) in conjunction with the length of the developmental season (Shapiro, 1975). Both of these external factors are known to affect the period of adult activity, and any explanation of adult flight periods which fails to incorporate or account for these factors is partial at best. For example, in one of the species, *Wallengrenia egeremet* (Scudder), latitude nicely explains the phenology of broods (Burns, 1985).

To date, evidence accumulated for or against competition as a structuring force in communities has utilized taxonomically diverse assemblages of species inhabiting geographically widespread and ecologically diverse communities (Schoener, 1983; Strong, 1984). Given the assumptions which underlie the premise of a structured community (i.e., stable gene frequencies controlling behavioral and morphological traits) it is unrealistic to expect to find resource partitioning in widespread, panmictic populations occupying ecologically diverse areas which vary with respect to the pool of potential competitors. Better communities for this type of investigation are those which are associated with rare and/or fragmented abiotic conditions (i.e., communities containing populations with very little or no genetic influx from other populations), and whose array of potential competitors are homogeneous. Representative communities include those found in serpentine barrens, bogs, fens, alpine meadows, natural ponds, and so forth. The most suitable potential competitors for this type of study are groups of closely related species, increasing the potential for competition due to similar ecological requirements. Examples of such communities of species are numerous, and amoung the lepidoptera include Heliconius butterflies (Gilbert, 1984), checkerspot butterflies (Ehrlich, et. al., 1975), wetland hesperiids (Shuey, 1985), and prairie Hesperia (McGuire, 1982).

If potential resource partitioning is identified I feel it is more likely a priori to be the result of; 1) random circumstances; 2) localized continuous interspecific competition for resources within closed populations; or 3) the spread of formerly localized populations in which resource partitioning had become genetically fixed during a past period of localized interspecific competition. Each of these scenarios makes predictions testable under field conditions using closed natural communities. If the apparent resource partitioning is the result of random or haphazard circumstances, observations upon several communities should reveal random patterns of resource partitioning including communities which demonstrate no partitioning. If resource partitioning is the result of localized continuous interspecific competition a series of communities should demonstrate various combinations of resource utilization patterns. (i.e., there should be several independent solutions to the resource partitioning problem which would superficially resemble random or haphazard patterns, but with all communities demonstrating resource partitioning). If the apparent resource partitioning developed at sometime in the past and was genetically fixed before the current range of the species was occupied, all of the communities should show the same answer to the resource partitioning problem.

While no research directly addresses these predictions, the few available studies of closed or nearly closed communities indicate that such work is feasible and likely to yield important results (Schoener, 1974, 1983). By quantitatively assessing the spectra of adult resources used under various "natural" combinations of potential competitors, baseline patterns can be documented for direct comparison. Once baseline data is in place, some types of communities are ideally suited for the introduction of "missing competitor(s)" to test for competition (e.g., small wetlands where appropriate host plants are usually present, and the missing potential competitor[s] usually occur nearby). The resulting shifts, or lack thereof, in the spectra of resources used after the introduction (assuming the proper control communities are maintained), should shed light on the basic question at hand: are the observed ecological differences between species the result of competitive interactions or are they the result of other biotic or abiotic factors?

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### The Trouble with Butterflies

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The existence in this and other journals documents that of the vast diversity of insects available, the butterflies is a group of animals very frequently studied. Butterflies are disproportionately the subject of notes, articles, and books. Virtually all butterfly books aimed at general audiences, if they say anything to justify themselves, state the case in very modest terms. Authors too numerous to cite mention the captivating sight of colorful butterflies on the wing.

Many professional biologists doing scientific research with butterflies can refer back to childhood interest in catching and collecting these animals. Research scientists among us, however, often make the claim that butterflies are better suited for scientific research purposes than are most other organisms. Such claims are commonly found in grant proposals. The separate points made in favor of butterflies are generally valid.

- (1) The taxonomy of butterflies is reasonably well-worked out.
- (2) Their geographic distributions are well known.
- (3) Their life cycles are usually understood.
- (4) Their ecological relationships are at least partly known.
- (5) They are conspicuous in diurnal flight and relatively easy to handle.
  - (6) Compared to vertebrates, they are small and have short life cycles.
- (7) Since many people, both professional and amateur, do research on butterflies, there often exists the critical intellectual mass necessary for scientific progress.

While these characteristics are helpful to the scientist, balance is lost by the failure to mention, let alone discuss frankly, those traits commonly found in butterflies which are a hindrance.

Perhaps the most disadvantageous trait is that one or more of the life stages of these holometabolous insects is almost always unobservable. It is also true that species with diapause stages are very difficult to work with in the laboratory and that specific ecological relationships, such as those involving larval food plants, are often unknown. Genetic systems are usually polygenic, electrophoretic, or unknown. Here I discuss the problems that butterflies commonly present to scientists.

In the worst cases, we are not even thinking about the difficult problems, but are simply proceeding with experiments on questions that seem tractable. Final answers to questions of causes of distributions 208 J. Res. Lepid.

and dynamics of populations must remain unavailable as long as one or more life stage is ignored as too difficult to work with. In the best cases, we are regularly designing and performing experiments that fail to overcome the problems inherent in our experimental organisms. We are rarely and sporadically publishing the negative results, so we are not evoking all of the peer comment possible.

### Unobservable Life Stage

Perhaps the only truly complete life history description (with a good physical description for each life stage) in the literature is Wright's (1983) for *Lycaena epixanthe*. The situation for population biology studies involving all life stages is similar. Very few complete life tables have been published for natural populations of butterflies (see Dempster 1983). I (White 1986) have found only seven butterfly life tables in the literature (Harcourt 1966, Dempster 1967, Watanabe 1976, and Watanabe & Omata 1978) in which each stage is represented by a sample size of more than ten individuals. This is so because one or more of the life stages is difficult or impossible to observe in the field. The reader is doubtless aware of some of the problems presented by his own research organism and may not care to hear about them from me. This is especially so since my own research organism has plenty of its own disadvantages. I will therefore discuss my own system.

The Bay Checkerspot butterfly, Euphydryas editha bayensis Sternitzky (1937), is one of the most thoroughly studied of insects (Ehrlich 1984), but only its adult stage is easily observed by the biologist (Fig. 1). Adult butterflies might seem easily observable, but even this life-stage puts the observer to great effort. Only in the 1981 study (Ehrlich et al. 1984) where three very experienced people worked virtually each day of the flight season is it thought that virtually all the male *Euphydryas editha* in one generation of one population (Jasper Ridge H) were captured (n = 316). Even in this case the authors estimated that only 162/221(73%) of the females were handled during the season. In the course of the twenty-five year study at Jasper Ridge (Stanford University's biological preserve) the estimated proportion of males handled has averaged 60% and has sometimes fallen as low as 30%. The proportion of females handled has always been smaller. These values are very good for field studies in general, but they nonetheless make it clear that even the most "apparent" life-stage of the Bay Checkerspot butterfly is partially unobservable. Each of the other life stages is more difficult to observe in nature.

The distribution of egg masses probably averages about one per ten square meters in denser populations, rising to one per two square meters in the best years (assuming five masses per female, maximum of 2000 females in JRH 1960–1984, area of 2 ha. = 20,000 sq m). Since the size of an egg mass is about 10 sq mm, the average proportion of the substrate

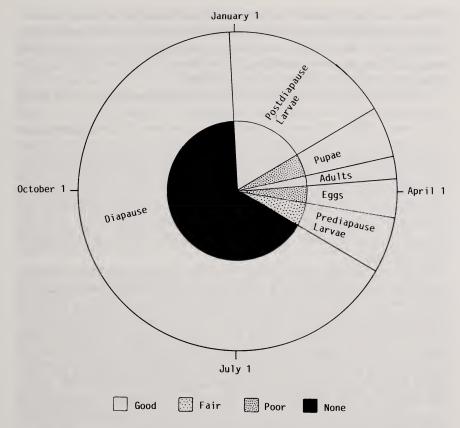


Fig. 1. The annual life cycle of *Euphydryas editha bayensis*, divided proportionately by length of life stages. The outer circle names the life stage. The inner circle indicates our current level of information.

covered by eggs is about  $0.000001 (10 \text{ sq mm}/10(1000 \text{ mm} \times 1000 \text{ mm}) = \text{one millionth})$ . Egg masses therefore have been and continue to be very difficult to monitor. Only one of the extant Bay Checkerspot populations is currently dense enough to allow numbers of egg masses to be found.

Prediapause larvae disperse in search of food as their annual food plants senesce, making accurate assessment of their fates extremely difficult. An exception occurs when larval growth is slower than "normal" relative to plant senescence schedules. When host plants senesce before the adult flight season ends, it is a certainty that more than 98% of the prediapause larvae will starve due to lack of edible plants (Singer & Ehrlich 1979).

Diapausing fourth instar larvae (4–20 mg, about 3–6 mm long) are hidden in the soil, sometimes under rocks, probably in peak densities of no more than one or two per square meter. This density would allow for  $40,\!000$  diapausing larvae at JRH (2  $\times$  20,000 sq m), a habitat where the maximum adult population has not exceeded 4000 (averaging about

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1200) in the past quarter century. Diapausing larvae are also mobile, making it possible for them to relocate if disturbed by would-be observers (Singer 1971). Small size, low density, and mobility have made field study of this stage impossible. In addition, high mortality in the laboratory makes study there very difficult.

Post-diapause larvae become visible to the trained eye as they reach sixth and seventh instars. When populations are dense (about one third of the years 1968–85) one can find 40 or more post-diapause larvae per hour in the last week of February. Since most larvae are on the barest areas of substrate I assume that many larvae go unobserved at any one time. Inactive larvae and those obscured by vegetation are unlikely to be seen. Post-diapause larval samples have been collected and parasitoid rates (Ehrlich 1965, White 1973, Stamp 1984), generally under 20%, are apparently unrelated to adult population size changes. I am currently investigating short-term growth and dispersal by using individually tagged larvae.

Pupae are almost never found. The few found have been within a sparse web holding together a few blades slender foliage. Mature larvae seem to "take a hike" just prior to pupation, probably making it harder for pupiphagous predators to find them. The behavior of pupating so as to remain unseen is clearly a form of crypsis. Crypsis is probably more important during pupation than during any other life stage because the pupa has the maximum digestible and assimilable biomass per individual. Only the prepupal larva briefly weighs more (about 25% more), and much of the difference is sclerotized (therefore undigestible) epidermal tissue and gut contents. Adult females at eclosion weigh about 75% of their freshly formed pupal weight. Adult males weigh only about 50% of their pupal weight and both sexes progressively lose unsclerotized tissue weight as their adult lives go on, making older butterflies less and less energetically rewarding to predators. The pupa is shorter and of greater diameter than the preceding mature larva and than the succeeding adult, so sclerotized surface area is minimized relative to potentially digestible volume. During the pupal stage larval tissues are being degraded into the universal biochemical building blocks (easily usable by any potential consumer) in order to build new, adult tissues. In addition, the sclerotized tissue is relatively segregated from the contents and therefore easy for a predator to separate from digestible contents. And, obviously, the pupa itself has virtually no behavioral means of defense other than by twitching.

Thus, the pupal stage is the most rewarding and the most defenseless life stage and we might expect pupiphagy to be important in the population biology of butterflies. Indeed, in 13 of 21 samples of pupal mortality of eight species of butterfly (White 1986, Smith 1986), mortality exceeded 50%. In 11/13 of those cases predation was the major factor. The only work on field mortality of  $Euphydryas\ editha$  pupae is my own (White 1986, and unpub.), and that depends on pupae placed artificially in the field. Ideal data would come from pupae formed naturally,  $in\ situ$ .

For the much studied Bay Checkerspot butterfly, we see that one stage (diapause, 65% of the duration of the life cycle) is quite intractable, three stages (egg, prediapause larva, and pupa) are so difficult to monitor that little is known of them, and two stages (adult and post-diapause larva) are readily observable (Fig. 1). Similar situations exist for most other butterfly species commonly studied.

### **Food Plants**

Considering all the work done on food plant relationships of populations of Euphydryas editha one would expect that the best studied populations, those of *E. e. bayensis* would be thoroughly understood. But we acquired significant new information in 1985, year 26 of the study. We have always been puzzled as to why postdiapause larvae in the lab should prefer the Eurasian weed, Plantago lanceolata, to their usual field plant, Plantago erecta. This past season I discovered that postdiapause larvae marked and released into different patches of lush, green Plantago erecta behaved very differently. Individuals of a group put onto a western exposure disappeared while those placed onto a northern exposure stayed put. In a replicate of the experiment, larvae on the western exposure moved an average of 2.5 meters in three hours while larvae on the northern exposure moved an average of only 0.5 m. The difference was due to the age or developmental state of the Plantago. The taller, more mature plants on the western exposure still showed no sign of browning or senescence. They were in the early stages of setting seed. Larvae paused to eat for short periods and then moved away.

Larvae on the northern exposure tasted the shorter, less mature plants there and kept right on eating. For many years biologists have been pulling up handfulls of the larger plants to feed their laboratory larvae. We have avoided the much harder-to-harvest, smaller plants, and we have thereby been providing almost inedible fare. Small wonder that the Eurasian weed was preferred.

### Conclusion

In terms of ecological relationships such as larval food plant, much progress has been made (compare Howe 1975 to Opler & Krizek 1984 and to Scott 1986), yet much remains to be done.

With respect to observational difficulty, butterflies are no worse than many other organisms studied. For instance, most of the interesting social interactions of many rodents occur underground, out of sight of the biologist. Similarly, root systems of plants have been difficult for plant ecologists to study (Cody 1986). Still, it is the responsibility of those working on butterflies to devote proportionately more time to the investigation and discussion of the more difficult life stages. Because the failure to discuss problem areas in print ultimatley retards progress, it would be beneficial for authors to include such discussions. More attention being thus focussed on problem areas ought to result in more

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experimental effort being spent there. Alternatively, much research could be switched to more tractable species (such as *Agraulis vanillae*).

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# A Response to Landing: On Factors in the Distribution of Butterfly Color and Behavior

Dennis D. Murphy

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I suspect that Dr. Landing's frustration with my critique of his collected works (1985 J. Res. Lep. 24: 376–379) exceeds by good measure my frustration with his reply (1986 J. Res. Lep. 25: 67–70), but since I have been misquoted where he has quoted me, and misinterpreted by him seemingly everywhere else, a response is warranted.

Two interconnected problems pervade Landing's reply (and his original publication) which thoroughly cloud his attempts to promulgate his possibly interesting ideas. One problem is his inability to cogently couch his arguments — from a 98-word second sentence to the use of the word "parenthetically" in parentheses. The other problem is even more exasperating. Landing refuses to play by the "rules" of scientific inquiry. In his reply, he buries errors of interpretation under the same muddled reasoning I complained of in his book. Therefore, I limit myself here to just a couple of points in that reply.

Landing states that I "object to the use of models" and that my definition of ecological niche "is inadequate for butterflies." I do not object to the use of models; what I argued was that his construct does not function as a model. It does not predict, does not simplify nature, and does not shed light on processes.

Regarding ecological niche, I noted that the term has a formal definition, in use since it was proposed by Hutchinson more than forty years ago. If the term is "inadequate," that is, does not describe the situation, then Landing should not use the term. By creating his own definition for the term and by not telling his readers, Landing simply confuses. If he feels the vertical sorting of butterflies by color is a key factor in the structuring of butterfly communities, then a term for that does exist. Factors acting on "each stage of the life cycle" are called niche components. The sum of individual niche components (perhaps, such as the vertical position of a certain butterfly species) make up the niche of a given species. Gilbert and Singer (1975, Ann. Rev. Ecol. Syst. 6: 365-397, following Owen 1959, Entomol. Gaz. 10: 27-38), for instance, define key niche components of butterflies as (1) larval food plants, (2) parts of host used, (3) times of appearance (phenology and voltinism), (4) habitats, (5) adult resources, and (6) parasite and predator escape. They note that these niche components interact in complex ways, and might have noted that each of these niche components could be subdivided and

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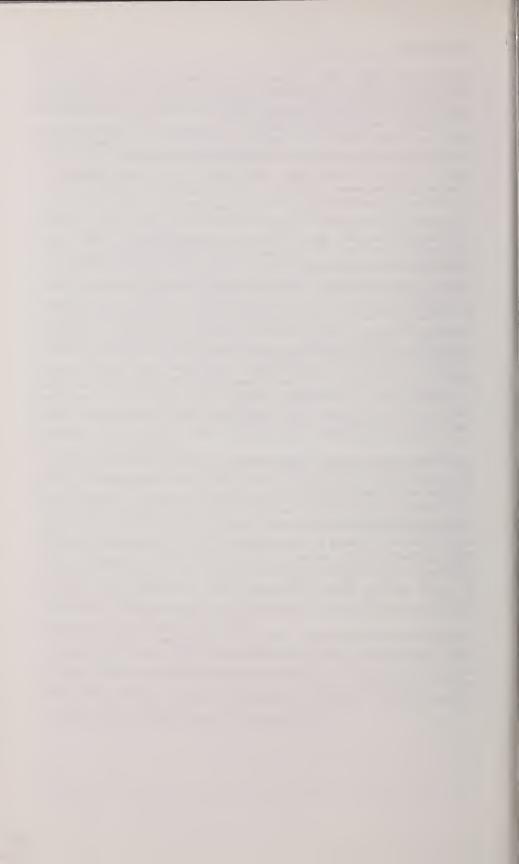
that other equally important components well might exist. Each individual niche component must be understood in order to understand the behavior of individual butterflies, the dynamics of their populations, and, ultimately, the structure of butterfly communities. Landing certainly presents no evidence in his treatment that "butterfly color" alone is the niche component which explains the structuring of communities.

Landing seems not to be particularly well-versed in butterfly biology in general. Many of his observations on mimicry were made by previous authors long ago. His statements on the "heat collecting capacity of different wing colors" are especially naive. Clench (1966, Ecology 47: 1021-1034) notwithstanding, butterfly wings are not radiators for hemolymph (e.g. see Watt 1968, Evolution 22: 437-458 and Kingsolver's review, J. Res. Lep. 24: 1-20, for a discussion of the role of wing color in thermoregulation). He, additionally, says that he does not see how nectar as a limiting resource could play a role in the distribution of butterfly "color types." Yet, all factors acting on the distribution of butterflies affect the frequencies of "color types" in specific habitats. Nectar resources can dramatically affect habitat suitability and population structure, and thereby the distribution of butterflies of certain colors in their physical environments, even for temperate zone butterflies which are thought to be relative generalists in their selection of adult food sources (Gilbert and Singer 1973, Amer. Nat. 107: 58-73; Murphy 1983, Environ. Ent. 12: 463-466; and Murphy et al. 1984, Oecologia 62: 269-271).

Finally, there is Landing's dumbfounding assertion that the discussion of Papageorgis's work (1975, Amer. Sci. 63: 522–532) in a general text somehow renders as facts the conclusions she drew in her original work. May I suggest that it is a fact that certain species tend to fly in certain places. That community structure of heliconiines and ithomines is largely determined by the co-occurrence of species sharing certain color patterns is a falsifiable hypothesis, hence subject to testing. That selection has "geared color pattern to height of flight in the vegetation because each pattern is most effectively cryptic at that level," is speculation which probably is not falsifiable. How would one develop an adequate test of that in the field?

In conclusion, I certainly hope that Dr. Landing withholds his promised 300 page manuscript-to-be until he can offer something more than circular reasoning and unsupported supposition in the guise of biological data. Then again, I do sort of look forward to an explanation of what Landing calls "intra-individual Muellerian mimicry." Landing doesn't consider that a "radical idea." I certainly do.





### INSTRUCTIONS TO AUTHORS

Manuscript Format: Two copies must be submitted (xeroxed or carbon papered), double-spaced, typed, on 8½ x 11 inch paper with wide margins. Number all pages consecutively and put author's name at top right corner of each page. If your typewriter does not have italic type, underline all words where italics are intended. Footnotes, although discouraged, must be typed on a separate sheet. Do not hyphenate words at the right margin. All measurements must be metric, with the exception of altitudes and distances which should include metric equivalents in parenthesis. Time must be cited on a 24-hour basis, standard time. Abbreviations must follow common usage. Dates should be cited as example: 4. IV. 1979 (day-arabic numberal; month-Roman numeral; yeararabic numeral). Numerals must be used before measurements (5mm) or otherwise up to number ten e.g. (nine butterflies, 12 moths).

Title Page: All papers must have the title, author's name, author's address, and any titular reference and institutional approval reference, all on a separate title page. A family citation must be given in parenthesis (Lepidoptera: Hesperiidae) for referencing.

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Name Citations and Systematic Works: The first mention of any organism should include the full scientific name with author (not abbreviated) and year of description. New descriptions should conform to the format: male: female, type data, diagnosis, distribution, discussion. There must be conformity to the current International Code of Zoological Nomenclature. We strongly urge deposition of types in major museums, all type depositions must be cited.

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TAXONOMY, PHYLOGENY, AND BIOGEOGRAPHY OF

# ASTEROCAMPA

Röber 1916 (LEPIDOPTERA, NYMPHALIDAE, APATURINAE)

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# Taxonomy, Phylogeny and Biogeography of *Asterocampa* Röber 1916

(Lepidoptera, Nymphalidae, Apaturinae)

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### **Preface**

The material presented here is taken from my dissertation entitled, "A taxonomic revision of *Asterocampa* Röber 1916 (Insecta, Lepidoptera, Nymphalidae)," accepted in partial fulfillment of a doctoral degree in entomology by the Graduate School of Texas A&M University, May 1985. Aside from corrections, I have added new and clarifying material in the past two years, largely as a result of morphological investigations of other closely related genera.

My special interest in hackberry butterflies stems from observations I made on insects inhabiting hackberry trees at the Brackenridge Field Station of the University of Texas in Austin, while I was a graduate student there. Many a day (and several nights) were spent observing larvae and adults in an attempt to figure out how the two resident species of *Asterocampa* and other hackberry insects partitioned resources. My move to Texas A&M University (systematic entomology) and choice of doctoral dissertation were direct outgrowths of those early studies.

The hackberry butterflies, *Asterocampa* Röber, are here taxonomically revised based on biological and morphological studies of all life stages of these insects. A new subspecies name is proposed for the Floridian population of *Asterocampa celtis* (Boisduval & Le Conte) which has mistakenly been called *A. alicia* (Edwards). There are conservatively four biological species of hackberry butterflies, based on field observations, preliminary laboratory hybridization studies, and morphological comparisons.

The geographic ranges of the species in the genus extend from Nicaragua and the Greater Antilles, north and westward through Mexico and the United States (except the Pacific Northwest) into southeastern Canada. The butterflies are typically found in close association with hackberry (Ulmaceae: *Celtis* spp.) which is their sole larval food plant.

Cladistic methodology was employed to construct the classification presented. *Asterocampa* is defined in relation to other apaturine genera. The evolution of the genus is discussed in the context of the distributions of the taxa. *Asterocampa* probably evolved in North America following its introduction and subsequent isolation from eastern Asia. There are 2 well-defined species groups in the genus, which utilize the host plant in different ways.

These studies would not have been possible but for the many people from whom I have received help or advice. I thank P. R. Ackery, C. R. Beutelspacher, F. M. Brown, H. R. Burke, J. M. Burns, J. R. Cate, J. P. Donahue, W. D. Duckworth, C. Durden, G. Ekis, J. F. Emmel, C. D. Ferris, L. E. Gilbert, D. W. Jenkins, K. Johnson, G. Lamas, L. D. & J. Y. Miller, R. W. Neck, S. J. Ramos, J. E. Rawlins, W. J. Reinthal<sup>†</sup>, F. Rindge, D. H. Riskind, R. K. Robbins, J. C. Schaffner, D. J. Schmidly, A.

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I gratefully acknowledge the assistance of L. G. Friedlander in all phases of this work.

### Introduction

Asterocampa Röber is a genus of North American butterflies, the members of which are known as hackberry butterflies. There are roughly a dozen species-level taxa of hackberry butterflies. Taxonomically, they belong in the family Nymphalidae (sensu latu) or in the Apaturidae, a closely related family of butterflies whose members are somewhat intermediate in morphology between the Nymphalidae (sensu strictu) and the Satyridae. There are about 20 apaturine genera, all in the Old World, except for the Nearctic Asterocampa and the Neotropical Doxocopa Hübner.

Asterocampa larvae feed on hackberry trees and shrubs (*Celtis* spp., Ulmaceae), from which the adult common name is derived. Hackberry butterflies occur from Nicaragua and the Greater Antilles north and westward through Mexico and the United States (except the Pacific Northwest) and into southeastern Canada, virtually everywhere their larval host plants occur.

Asterocampa was badly in need of revision, not having been broadly treated since the apaturine butterflies were catalogued in 1938 (Stichel, 1938). Recognizing this need, the late Dr. Walfried J. Reinthal studied hackberry butterflies over the last 3 decades with the intention of revising the genus. His extensive fieldwork in the United States and the Caribbean, coupled with rearing and breeding studies, gave him a unique appreciation for the diversity within the genus. Although he was never able to summarize his findings for publication, authors treating these butterflies in the last 20 years have relied on his extensive knowledge of the genus in their books and articles (Brown, 1967; Comstock, 1961; dos Passos, 1964; Howe, 1975; Johnson and Nixon, 1967; Miller and Brown, 1981, 1983; Pyle, 1981). As a consequence, the best evidence supporting the present classification of Asterocampa is found in the collection of reared specimens, notes and correspondence of Dr. Reinthal. This collection was willed to the Carnegie Museum of Natural History.

There are three purposes to my revision of hackberry butterflies. First, the recognizable species-level taxa of *Asterocampa* are defined, described, ranked and related. Second, the genus is defined by synapomorphic characters (Hennig, 1966; Wiley, 1981). A testable hypothesis is made about its closest relatives, or sister group. Third, ecologic and biogeographic hypotheses are formed, relating the character diversity and distributions of hackberry butterflies.

My approach to this revision is cladistic in the sense of Wiley (1981). Morphological and behavioral characters of all developmental stages of hackberry butterflies are surveyed. As many characters as could be reliably compared with those found for other apaturine genera are used as a starting point from which to define *Asterocampa*. Material from major North American museums was borrowed for examination. All but one taxon was reared so that living specimens were studied for virtually all hackberry butterflies in all their life stages.

### **Taxonomic History**

The taxonomic history of hackberry butterflies is complex for the size of their genus. Taxa presently assigned to *Asterocampa* have resided in a half dozen genera over the years. Application of species-level names to these taxa has been a source of controversy for over a century. The genus *Asterocampa* was proposed by Röber in 1916 in Seitz's *Macrolepidoptera of the World*, the first name to include just the North American New World apaturine butterflies.

A sketch of nomenclatural changes through major North American works is given in tabular form (Table 2) below the table of Röber's included taxa (Table 1). For a more complete treatment of the nomenclatural history of hackberry butterflies the reader should refer to my dissertation.

The common names applied to species and subspecies now included in *Asterocampa* are an interesting sideline to the history of the group. Riley (1873) first called the genus "hackberry butterflies." For a complete treatment of these names the reader should refer to my dissertation.

Table 1. Hackberry butterflies treated by Röber in Seitz (1916).

Date	Taxon as described	Taxa, according to Röber (1916)
1793	Papilio lycaon Fabricius	Asterocampa lycaon Fab.
1793	Papilio herse Fabricius	A. lycaon Fab.
[1828]	Doxocopa idyja Geyer in Hübner	A. lycaon form idyja Hbn.
[1835]	Apatura celtis Boisduval & Le Conte	Asterocampa celtis Bsd.
[1835]	Apatura clyton Boisduval & Le Conte	A. lycaon. Fab.
1864	Apatura argus Bates	Asterocampa argus Bates
1868	Apatura alicia Edwards	Asterocampa alicia Edw.
1868	Apatura proserpina Scudder	A. lycaon Fab.
1874	Apatura leilia Edwards	Asterocampa leilia Edw.
1876	Apatura clyton var. ocellata Edwards	A. lycaon aberr. ocellata Edw.
1876	Apatura clyton var. flora Edwards	A. lycaon form flora Edw.
[1878]	Apatura antonia Edwards	A. leilia [form] antonia Edw.
1883	Apatura antonia var. montis Edwards	A. celtis [form] montis Edw.
1911	Chlorippe clyton var. texana Skinner	A. lycaon Fab.
1912	Doxocopa argus form armilla Fruhstsorfer	A. argus [color f.] armilla Fru.

Table 2. Comparison of American classifications of hackberry butterflies.

Skinner, 1911	McDunnough, 1938	Miller & Brown, 1983	Present revision
<ol> <li>celtis         <ul> <li>a. alicia</li> <li>b. antonia</li> </ul> </li> <li>c. leilia</li> </ol>	<ol> <li>celtis         <ul> <li>a. alicia</li> <li>b. antonia</li> <li>c. montis</li> </ul> </li> <li>leilia</li> </ol>	<ol> <li>celtis</li> <li>alicia</li> <li>antonia</li> <li>montis</li> <li>leilia</li> <li>cocles</li> </ol>	<ol> <li>celtis         <ul> <li>reinthali</li> <li>antonia</li> </ul> </li> <li>leilia</li> </ol>
2. clyton a. flora b. texana	3. clyton a. flora b. texana c. subpallida	6. clyton 7. flora 8. texana 9. subpallida 10. louisa [11. idyja] [12. argus]	3. clyton a. flora b. texana c. louisa 4. idyja a. argus

Table 3. Classification of Asterocampa Röber.

Asterocampa Röber, 1916. In Seitz, Großschmett. Erde, 5: 549. Typespecies by subsequent designation of D. M. Bates, 1926. Entomol. News, 37: 154, Apatura celtis Boisduval and Le Conte, [1835]. Hist. gen. iconogr. lépid. amér. sept.: 210.

- 1. **celtis** (Boisduval and Le Conte, [1835]) *APATURA*. Hist. gen. iconogr. lépid. amér. sept.: 210. TL "Géorgie", probably northwest of Savannah, perhaps in Screven County, Georgia. Type based on Abbot drawing, the model for which has not been found.
  - a. c. celtis (Boisduval and Le Conte, [1835]). [as above]
    - = alicia (W. H. Edwards, 1868) *APATURA*. Butts. N. Amer., 1: [135]. TL vic. New Orleans, Louisiana. Types lost; the figures in W. H. Edwards, 1868. Butts. N. Amer., 1: pl. Apatura I may be considered to represent types.
    - = **alba** (W. G. Wright, 1905) *APATURA*. Butts. W. Coast: 58. Validating excluded name "Celtis ab. a. Alb." (H. Strecker, 1878) *APATURA*. Butts. moths N. Amer.: 145. TL not stated, but may be taken as Coalburgh, West Virginia. Type represented by Edwards' figure, 1875. Butts. N. Amer., 2: pl. Apatura I, fig. 5.
  - b. c. reinthali Friedlander, 1987. [this work] TL Ocoee, Florida. HT to be placed in CMNH.
  - c. c. antonia (W. H. Edwards, [1878]). APATURA. Field and Forest, 3:103. TL - vic. Norse, Bosque Co., Texas, restricted by F. M. Brown, 1967. Trans. Amer. Entomol. Soc., 93: 377-378. LT in CMNH, designated by F. M. Brown, 1967. Trans. Amer. Entomol. Soc., 94: 379.

- = montis (W. H. Edwards, 1883) *APATURA*, Papilio, 3:7. TLvic. Ft. Grant, Graham Mtn., Cochise Co., Arizona. LT in CMNH, designed by F. M. Brown, 1967. Trans. Amer. Entomol. Soc., 93: 382.
- 2. **leilia** (W. H. Edwards, 1874) *APATURA*. Trans. Amer. Entomol. Soc., 5: 103. TL "Camp Lowell and in Sonoto Valley, Arizona". LT in CMNH, designated by F. M. Brown, 1967. Trans. Amer. Entomol. Soc., 93: 385.

= cocles (Lintner, (1885)) *APATURA*. Papilio, 4: 141. TL - Hidalgo, Texas. LT in CMNH [designated in this work].

- 3. **clyton** (Boisduval and Le Conte, [1835]) *APATURA*. Hist. gen. iconogr. lépid. amér. sept.: 208. TL "méridionales des États-Unìs", probably Screven County, Georgia. Type based on Abbot drawing, the model for which has not been found.
  - a. c. clyton (Boisduval and Le Conte, [1835]). [as above]
    - = ocellata (W. H. Edwards, 1876) *APATURA*. Butts. N. Amer., 2: [245]. TL Coalburgh, West Virginia. LT in CMNH, designated by F. M. Brown, 1967. Trans. Amer. Entomol. Soc., 93: 387.
      - = proserpina (Scudder, 1868) *APATURA*. Proc. Boston Soc. Nat., Hist., 11: 401. TL Iowa. Type misplaced; not in MCZ. = nig (J. B. Smith, 1903) *APATURA*. Check list Lepid. bor. Amer.: 4. Validating excluded name "Clyton ab. b. Nig." (H. Strecker, 1878) *APATURA*. Butts. moths N. Amer.: 145. TL Berks Co., Pennsylvania. HT in Strecker Coll. presently located at AME.
  - b. c. flora (W. H. Edwards, 1876) APATURA. Butts. N. Amer., 2: [247]. TL Palatka, Florida. LT in CMNH, designated by F. M. Brown, 1967. Trans. Amer. Entomol. Soc., 93: 389.
  - c. texana (Skinner, 1911) CHLORIPPE. Trans. Amer. Entomol. Soc., 37: 214. TL Round Mt., Texas. HT in CMNH.
    = subpallida (Barnes and McDunnough, 1913) CHLORIPPE. Contr. Nat. Hist. Lepid. N. Amer., 2: 99. TL Babaquivera [sic] Mtns., Pima Co., Arizona. LT in USNMNH [designated in this work].
  - d. c. louisa Stallings and Turner, 1947. Entomol. News, 58: 38. TL -Pharr, Texas, HT in YPM.
- 4. **idyja** (Geyer, [1828]) *DOXOCOPA*. *In* Hübner, Samml. exot. Schmett., 3: pl. [13]. TL Cuba. Type presumably lost; the figures considered to represent type.
  - a. i. idyja (Geyer). [as above]
    - = **padola** (Fruhstorfer, 1912) *DOXOCOPA*. Entomol. Rundschau, 29: 14. TL Haiti. STs in ZMHU, Berlin.
  - b. i. argus (H. W. Bates, 1864) APATURA. Entomol. Month. Mag.,1: 130. TL Motagua Valley, Guatemala. HT in BM.

### $\textbf{Keys for the Identification of Species and Subspecies of} \ A \textit{sterocampa}$

### EGGS:

1.	Eggs deposited singly or in small clusters (1-50); with wrinkling
	of chorion between longitudinal ribs and with aeropyles along
	whole length of ribs to base (Pl.5, fig. B; Pl.6, fig. C; Pl.8, fig. C)
	2
1'.	Eggs deposited in large tightly packed clusters forming
	multilayered egg mass, often 3- to 5-layered (50-500); without
	wrinkling of chorion between longitudinal ribs and lacking
	aeropyles on lower half of ribs (Pl.13, figs. C, D; Pl.14, figs. C, D;
	Pl.16, fig. B)
2.	Eggs deposited on tree-like hackberry species (Celtis
	occidentalis, C. tenuifolia, C. laevigata, C. lindheimeri, C.
	reticulata)
2'.	Eggs deposited on spiny hackberry species (Celtis pallida) 4
3.	Eggs deposited on host plant from eastern North America (east
	of 100°w. longitude)
3'.	Eggs deposited on Celtis reticulata (west of 100°w. longitude)
•	
4.	Eggs with aeropyles not reduced (Pl.6, fig. C)
4'.	Eggs with extremely small aeropyles (Pl.8, fig. C)
5.	Eggs occurring in eastern North America but not found in
	peninsular Florida, coastal Georgia or South Carolina
5'.	Eggs on Celtis laevigata in peninsular Florida, coastal Georgia
	or South Carolina
6.	Eggs found north of Tropic of Cancer
6'.	Eggs found south of Tropic of Cancer
7.	Eggs deposited on Celtis reticulata, C. lindheimeri or C. laevigata,
	found in central, south or west Texas, Mexico or Arizona
7'.	Eggs deposited on Celtis laevigata, C. occidentalis or
	C. tenuifolia, found in east and northeast Texas, northward and
	eastward9
8.	Eggs found in northeastern Mexico or lower Rio Grande Valley
	of Texas
8'.	Eggs found in south-central or west Texas, north-central Mexico
	around the edges of the Chihuahuan desert, or southeastern
	Arizona
8".	Eggs found in northwestern Mexico (central Sonora)
9.	Eggs occurring in eastern North America but not found in

	peninsular Florida, coastal Georgia or South Carolina
9'.	Eggs on Celtis laevigata in peninsular Florida, coastal Georgia
	or South Carolina
10.	Eggs occurring in Mexico or Central America
10′.	Eggs on Celtis trinervia in the Greater Antilles
	Asterocampa idyja idyja
LAF	RVAE:
1.	Larvae not aggregated as early instars (except diapausing third
1.	instars); with antler scolus AB5 (Fig. 1; Pl.7, figs. A, C; Pl.10,
	figs. A, C; Pl.11, figs. A, C, E) at most half the length of head
	scolus L1 (first instar larvae with dark brown or black head
	capsules, found in small numbers associated with small egg
	clusters); never longitudinally banded, but usually striped with
	lines and crenations of light yellow
1′.	Larvae gregarious as first 3 instars; with antler scolus AB5 (Fig.
1.	
	1; Pl.15, figs. A, B; Pl.16, figs. C-E) more than half the length of head scolus L1 (first instar larvae generally with light brown or
	tan head capsules, found in large numbers associated with large
	egg mass); often longitudinally banded with light yellow and
0	green
2.	Larvae not on Celtis pallida; mature larva usually marked with
	yellowish spots anterodorsally and zigzag (crenated) yellowish
01	line laterally on abdominal segments
2'.	Larvae on Celtis pallida, mature larva usually marked with only
0	dorsolateral and subspiracular yellowish lines on body
3.	Larvae exceptionally with vestigial antler scolus AB5; usually
0.1	found on Celtis reticulata Asterocampa celtis antonia
3'.	Larvae usually with vestigial antler scolus AB5; usually found
	on Celtis laevigata, C. occidentalis, or C. tenuifolia
	eastern subspecies of Asterocampa celtis
4.	Larva found in south Texas or northeastern Mexico; mature
	larva with black head marked with yellowish green
4'.	Larva found west of 100° west longitude, or mature larva with
	brown head marked with green and yellowish white
5.	Larvae without black anal horns; generally found north of
	Tropic of Cancer
5'.	Larvae usually with black anal horns; found in Mexico, Central
	America and Greater Antilles
	subspecies of Asterocampa idyja

6.	Larvae generally not banded with yellow and green; usually found on <i>Celtis reticulata</i> in Texas, Mexico or Arizona
6′.	Larvae generally banded with yellow and green; usually found on <i>Celtis occidentalis</i> , <i>C. laevigata</i> or <i>C. tenuifolia</i> in eastern
_	United Stateseastern subspecies of Asterocampa clyton
7.	Larvae found in northeastern Mexico or lower Rio Grande Valley of Texas (sometimes with rudimentary banding, often
	colorful, with dark heads and yellow and green bodies)
	Asterocampa clyton louisa
7'.	Larvae found in south-central or west Texas, north-central
	Mexico around the edges of the Chihuahuan desert, or southeasten Arizona (usually mostly green with whitish
	markings and only a small dark brown spot anteriorly on the
	antlers)
	Asterocampa clyton texana
PUI	PAE:
1.	Pupae with rather pointed pyramidal head prologations; dorsal
	crest not abrupt from thorax to abdomen, with blunt spines
	anteriorly on abdominal segments 3-8 (Pl.19, figs. G-J; Pl.11,
1′.	fig. F; Pl.12, fig. D)
1.	often rising abruptly at third abdominal segment, generally
	with sharp spines anteriorly on abdominal segments 3-8 (Pl.19,
	figs. K, L)
2.	Pupae with bed of cremastral hooks extending to end of
	sustainers in "Y"-shaped pattern; head prolongations long
2′.	Pupae with bed of cremastral hooks extending only half way to
	sustainers (Pl.12, figs. D, E; Pl.19, fig. J); head prolongations
	very short
3.	Pupae without shortened metanotum dorsally
3′.	
٥.	Asteocampa idyja subspecies
AD	ULTS:
1	Forevir as with dealth become limbal anotain call Cult assessed
1.	Forewings with dark brown limbal spots in cell Cu1, eyespot present on hindwing anal cup ventrally (cell A2 limbal spot)
	(Fig. 2); male genitalia with saccus and aedeagus usually less
	than twice length of valves, uncus shallowly indented; female
	genitalia with short ductus (Figs. 3, 6), signa usually present 2

1'.	Forewings without dark brown limbal spot in cell Cu1 (although spots might be narrowly ringed in dark brown), no eyespot on hindwing anal cup ventrally (Fig. 2); male genitalia with saccus and aedeagus at least 2 times length of valves, uncus narrowly	
	notched; female genitalia with long ductus (Figs. 6, 7), signa usually absent	5
2.	Forewings without broken basal discal bar; terminal dorsal brush with straight hair-scales (Pl.21, figs. A-C)	
		1
2'.	Forewings with broken basal discal bar (forming 2 spots);	
	terminal dorsal brush with recurved hair-scales	3
3.	Forewing with dark brown limbal spot in cell M3, both it and Cu1 with pupils, limbal spot Cu1 about equal in size to M3, or even smaller (Pl.19, figs. M, N; Pl.20, figs. G-O)	
		a
3′	Forewing without dark brown limbal spots in cell M3 or with at	Ī
	most posterior portion of spot M3 narrowly ringed with brown,	
	limbal spot Cu1 generally larger than M3 and unpupilled	1
4.	Not especially large (average FW costal length 24 mm (males),	
	27 mm (females)); pupils of limbal spots not particularly large or	
	colorful, pupil of spot Cu1 of FW centered, spot M1 of HW round	
	to oval and not elongated into a point laterally (Pl.20, figs. A-C)	•
.,		5
4′	Noticeably large (average FW costal length 29 mm (males),	
	31 mm (females)); pupils of limbal spots large and light blue or	
	blue green, spot Cu1 of FW lateralized, spot M1 of HW	
	asymmetrically elongate with crescentic pupil (Pl.20, figs. D-F)	
_		Ì
5.	Postmedian spots in normal zigzag positions (Fig. 2), those	
	anterior in forewings lying between end of discal cell and limbal	_
	spots	j
5'.	Postmedian spots shifted basally in anterior portion of	
_	forewings, next to end of discal cell (Pl.22, figs. J, L)	,
6.	Limbal spot Cu1 of forewing usually narrowly ringed with dark	
	brown, neither sex noticeably dimorphic in color, usually a high	
	percentage of females with hindwing limbal spots ventrally not	
	Some rung on prossou	7
6′.	Limbal spots Cu1 of forewing virtually never ringed with dark	
	brown, both sexes often exhibiting dark and light color phases,	
	ventral hindwing limbal spots in females usually fully	
	expressed	3
7.	Ground color of apical forewings and dorsal coloration of	
	antennae brown or orange, not black; found in south-central and	
	west Texas, in foothills of the Chihuahuan desert and in	
	southeastern Arizona (not found in lower Rio Grande Valley of	
	Texas and southward into northeastern Mexico) (Pl.21.	

figs. M-O; Pl.22, figs. A-C)

Asterocampa clyton texana

- 7.' Ground color of apical forewings and dorsal coloration of antennae black; found in lower Rio Grande Valley of Texas and southward into northeastern Mexico (Pl.19, fig. O; Pl.22, figs. D-F).....
- 8. Not especially large (average FW costal length 25 mm (males), 31 mm (females)); apical ground color of forewings tan to

brownish orange, light and dark color phase individuals present in varying percentages, hindwing limbal spots ventrally usually fully expressed (Pl.21, figs. D-I); not found in peninsular Florida, coastal Georgia or south coastal South Carolina......

......Asterocampa clyton clyton

- 9. Occur in Mexico or Central America; individuals usually have postmedian spots coalesced into golden band across FW, dark phase individuals not exhibiting this feature (Pl.22, figs. G-I) ......

......Asterocampa idyja argus

### Species and Subspecies Concepts of Hackberry Butterflies

Hackberry butterfly species were investigated within the context of the concept of biological species. Different species are said to be reproductively isolated from one another and populations of a single species are not, even though these populations might be allopatric or allochronic with regard to one another. This study is admittedly one of morphology and behavior, but very little of the latter was actually observed that would give needed evidence in this discussion. Molecular techniques involving the following of genetic markers through natural and laboratory breeding experiments are needed to refine what is postulated here.

Questions asked here are: 1) Do sympatric, synchronic populations of reputedly different species of hackberry butterflies interbreed in the field or the laboratory? 2) Do allopatric populations of what are currently held as species interbreed in the laboratory? 3) Are there either morphological or behavioral characteristics of any of the hack-

Ocoee, Florida

berry butterflies that might reasonably prevent them from interbreeding with other such populations (isolating mechanisms)? 4) Are there "hybrid populations" to be found in the field that offer evidence of genetic exchange between allopatric (or stasipatric) populations?

Viewed cladistically, the ability to interbreed is a character shared before speciation and not necessarily lost at speciation (symplesiomorphy). Only the inability to interbreed "in the wild" is held as acceptable as an indication that the respective populations under consideration belong to different species. The problems associated with allopatric and allochronic populations being compared or tested for the ability to interbreed have often been noted (e.g., Ehrlich, 1961). It is the opinion here that obstructions to interbreeding owing to differences in the organisms (and not the testing conditions) might serve to indicate respective specific status of the different populations being tested.

The known distributions of taxa studied in this revision are presented graphically in Plates 1-4. *Asterocampa celtis* and *A. clyton* are broadly sympatric over much of their respective ranges. Both of these species are sympatric with *A. leilia* over much of its range.

The degrees to which organisms are reproductively isolated have been argued to greater and lesser extents to indicate biological species (e.g., Mayr, 1969; H. H. Ross, 1974). One can only speculate whether or not a small degree of genetic exchange will lead the populations to speciation, or whether or not climatic or other conditions might change soon enough to affect their status (in either direction). A conservative approach has been taken in this revision. Unless it can be shown that the populations at hand are probably reproductively isolated, they are considered to be conspecific.

Sympatric and at least partially synchronic populations of hackberry butterflies are listed in Table 4.

Table 4. Sympatric populations of hackberry butterflies and examples of localities in which they can be found.

Localities	Populations of Hackberry Butterflies
wash at base of mountain in southeastern Arizona	A. leilia, A. celtis antonia ("montis"), A. clyton texana ("subpallida")
creek bottom in the chaparral of south Texas	A. leilia ("cocles"), A. celtis antonia, A. clyton texana or A. clyton louisa
Knoxville, Tennessee, or just about anywhere in e. U. S.	A. celtis celtis, A clyton clyton
south of New Orleans, Louisiana	A. celtis celtis ("alicia"), A. clyton clyton (form similar in appearance

to A. c. flora)

A. celtis reinthali, A. clyton flora

No interbreeding of butterflies from different populations at any of these and other localities was ever observed. Intra-population matings have been observed in the field for all the taxa in Table 4. Behavioral differences among sympatric populations were observed at these sites, which might help explain why no inter-pairings were seen.

Sympatric hackberry butterflies seem to be ecologically separable along 2 lines. The first line is exemplified by *A. leilia*. It has its own particular species of host plant which grows in a slightly different habitat than hosts used by other hackberry butterflies at a given site.

Males of hackberry butterflies perch within and rarely patrol a small area usually containing the larval food plant (Austin, 1977; Scott, 1975; personal obs.) and intercept virtually all passers-by in search of females. This is reasonable because virgin females emerge from pupal cases on the larval food plants and visit food sources near the future oviposition sites. However, in the case of *A. leilia*, the micro-habitat in which males perch is generally the ground in a dry wash. Males of other species of *Asterocampa* at the site would more likely be perched on trees growing in the wetter parts of the wash and would investigate different passers-by.

By far the most likely micro-habitat in which different species would be found together is at a rich food source such as a sap ooze on mesquite. Individuals at the ooze would be of both sexes but the females would have generally been previously mated and plugged.

The second line of ecological evidence for habitat partitioning by hackberry butterflies stems from the time of day the different species are active. This is best seen by times in which males from different sympatric populations are involved in courtship. In virtually every instance of observation, peak activity of one would be at mid-day and the other in the evening. It is worth putting forward the hypothesis that members of the Clyton group are active at higher temperatures than those of the Celtis group. In more southern localities one generally finds individuals of the Clyton group active at mid-day and those of the Celtis group active in the evening. The situation seems to be reversed in more northern localities, as individuals of the Celtis group are active at mid-day while individuals of the Clyton group are active in the late afternoon. It is rare to find males of different populations actively engaged in courtship at the same time and place.

A possible third instance of ecological separation stems from the observation that males of the Celtis group are often found within the canopy of the forest, whereas males of the Clyton group are more often found on the outside of the canopy. This difference might also be due to behavioral differences related to temperature.

A possible fourth ecologically important difference between sympatric populations of hackberry butterflies, one that also relates to courtship, is the difference in coloration in adults of the species. The only case in which there are two phenotypically very similar species occurring

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together is that of A. leilia and A. celtis antonia from Arizona to southern Texas.

A more complete study of the genetic differentiation of the hackberry butterflies such as was done by Hafernik (1982) for the North American buckeye butterflies (Nymphalidae: *Junonia* spp.) was not possible within the limitations of this revision. However, some data on the ability of different populations to exchange genetic information was found through hybridization studies. A complete regimen of crosses within and between different species, with the associated data of viabilities for each life stage was not attempted.

Laboratory populations were established for crossing, including the following taxa from the given localities: A. celtis antonia (Eddy Co., N Mex.) (virgin females challenged with wild males of A. celtis celtis from Brazos Co., Texas); A. clyton louisa (Hidalgo Co., Texas) (virgin females challenged with wild males of A. clyton clyton from Brazos Co., Texas); A. clyton clyton (Brazos Co., Texas) (challenged with reared individuals of A. celtis celtis (Brazos Co., Texas)); A clyton texana (Menard Co., Texas) (challenged with virgin males of A. celtis antonia (Eddy Co., N. Mex.). Only the first 2 crosses were successful, and the adult hybrid butterflies were reared.

Individuals of the following populations were reared and subjected to breeding challenges: A. celtis antonia (Travis Co., Texas) (by A. clyton texana (Travis Co., Texas)); A celtis celtis (Brazos Co., Texas) (by A. clyton clyton (Brazos Co., Texas)); A celtis antonia (Jeff Davis Co., Texas) (by A clyton texana (Jeff Davis Co. Texas)); A celtis antonia form "montis" (Pima Co., Arizona) (by A. clyton texana ("subpallida") (Pima Co., Arizona)); A clyton flora (Alachua Co., Florida) (by A. celtis reinthali (Alachua Co., Florida). None of these attempted crosses were successful.

In similar studies conducted by Dr. Walfried J. Reinthal (unpublished data) the following crosses (with back-crosses) were obtained: *A. celtis antonia* (Woodward Co., Oklahoma) (by *A. celtis antonia* ("montis") (Graham Co., Arizona)); *A. celtis antonia* (Palo Pinto Co., Texas) (by *A. celtis celtis* (Bibb Co., Georgia)). Attempts by him to cross members of the Clyton group with those of the Celtis group, like those of this author and many amateur breeders of butterflies, failed.

Successful crosses (viable adults reared in quantity) have been attained for the pairs of hackberry butterflies listed in Table 5.

Hybrid adult butterflies are phenotypically intermediate in characters used in that stage to define the parental types. This observation prompted the search (actually a feed-back loop) for similar looking wild butterflies in geographic areas between adjacent taxa. If one believes that observed intermediate phenotypes are indicative of hybridization in the field (not necessarily true!), there is hybridization between many pairs of taxa. In some cases there are zones of presumed hybridization between taxa in bands of many hundreds of kilometers long with varying thicknesses. These hypothesized bands of intergradation need

Table 5. Successful crosses between taxa of Asterocampa.

Challenged Female	Chal	lenging Male	Breeder
A. celtis antonia ("montis") A. celtis antonia	X X	A. celtis antonia A. celtis antonia ("montis")	Reinthal Reinthal
A. celtis antonia	X	A. celtis celtis	Friedlander, Reinthal
A. celtis celtis	X	A. celtis antonia	Friedlander, Reinthal
A. clyton louisa	X	A. clyton clyton	Friedlander

documentation by genetic means. One such band between subspecies of *A. celtis*, extends from near San Antonio, Texas to northwestern Nebraska, zigzagging its way through Oklahoma, Kansas and Colorado. Notably, in Austin, Texas and Denver, Colorado, populations of *A. celtis* exhibit the whole range in phenotypes between *A. celtis celtis and A. celtis antonia*. Similar zones of intergradation occur for the pairs of hackberry butterflies shown in Table 6.

Table 6. Pairs of hackberry butterflies for which populations showing intermediate characters have been observed in geographically intermediate areas.

Taxa: 1 A clyton texana	A. clyton texana ("subpallida")	Location of Intermediates Chihuahuan desert edges
A. clyton texana	A. clyton louisa	upper Rio Grande Valley
A. clyton texana	A. clyton clyton	e. Texas to e. Kansas
A. clyton clyton	A clyton flora	coastal Georgia, Florida panhandle to Louisiana
A. celtis antonia	A. celtis antonia ("montis")	central New Mexico, w. Texas
A. celtis antonia	A. celtis celtis	central Texas to nw. Nebraska
A. celtis celtis A. celtis celtis	A. celtis celtis ("alicia") A. celtis reinthali	e. Texas to s. Mississippi coastal Georgia, Florida panhandle

Nothing is known about the ability of either *A. leilia* or *A. idyja* to interbreed with other hackberry butterflies. It is possible that *A. leilia* could form hybrids with *A. celtis antonia*, but no wild intermediate butterflies have been called to anyone's attention. It is also possible that

A. clyton texana in one of its forms could come into contact with and possibly interbreed with A. idyja argus in either northeastern or northwestern Mexico. There are no intermediate forms known. To my knowledge, A. idyja idyja has not been reared during the past 50 years. In summary, the presumed interfertile taxa are presented in Table 7.

Table 7. Interfertile taxa (4 species) of hackberry butterflies.

Celtis group	Clyton group
A. celtis antonia A. celtis antonia (= "montis") A. celtis celtis A. celtis celtis (= "alicia") A. celtis reinthali A. leilia A. leilia (= "cocles")	A. clyton texana A. clyton texana (= 'subpallida") A. clyton louisa A. clyton clyton A. clyton flora A. idyja idyja A. idyja argus

Populations of infraspecific rank which are well defined geographically and distinguishable by some other set of characters are called separate subspecies in this revision. The subspecies is the lowest ranked taxon.

If such a population shows a gradual cline or a step-cline over a long distance with its neighbor, it is considered as not being well defined geographically. The Texan and eastern Mexican populations of Asterocampa leilia and the Rio Grande Valley (Texas, Mexico) population of A. celtis antonia are not considered subspecies in this revision. These populations have the informal names of "cocles" and "mexicana," respectively. I consider these as being taxa worth referring to by separate names, but not worthy of separate, valid, scientific names. Other distinctive populations of hackberry butterflies at the edges of their respective species' ranges include "montis" and "subpallida" in Arizona. Many other such populations exist but have not been given names. These are probably best handled by giving the locality of the population in question when discussing it, for example, "the Lake Roosevelt, Arizona, population of Asterocampa celtis antonia."

#### Materials and Methods

#### SPECIMENS:

Specimens from virtually all instars of all life stages and both sexes from each recognizable population of hackberry butterflies have been examined for characters of use in description and definition of taxa. Over 10,000 adult specimens were examined covering all known taxa from a dozen collections as listed below (Table 8). The extensive private collections of R. O. Kendall and W. J. Reinthal have also been studied.

Well over a total of 1,000 specimens of immatures stages from all taxa have been examined. Most of the latter were obtained through rearing.

Acronyms designating institutions are from Heppner and Lamas (1982).

Table 8. Institutions from which specimens were borrowed.

Acronym	Institution
AME	Allyn Museum of Entomology, Sarasota, Florida
AMNH	American Museum of Natural History, New York, New York
BMNH	British Museum (Natural History), London, United Kingdom*
CMP	Carnegie Museum of Natural History, Pittsburgh, Pennsylvania
FMNH	Field Museum of Natural History, Chicago, Illinois
FSCA	Florida State Collection of Arthropods, Gainesville, Florida
MNHP	Museum National d'Histoire Naturelle, Paris, France*
TAMU	Texas A&M University, College Station, Texas
UNAM	Universidad Nacional Autonoma de Mexico, Mexico, Mexico
USNM	National Museum of Natural History, Washington, D. C.
ZMHU	Zoologisches Museum, Humboldt Universität, Berlin, Germany (DDR)

\*correspondence about specimens

Whereas adult butterfly specimens can be found in great numbers among museums and private collections, specimens of immature stages are few and scattered. It was therefore necessary to collect immature stages for almost all of the taxa in this study. Most of the individual specimens of immature stages examined were reared by the author.

# NOMENCLATURE OF CHARACTERS:

Color descriptions were made from direct observation of live and preserved specimens and from color photographic slide transparencies taken of live material. Color names used in this work are those used in ordinary description compared with a standardized close approximation matched in the National Bureau of Standards color dictionary (Kelly and Judd, 1976).

Nomenclature used to describe the morphology of immature stages was taken from a variety of sources, including Kuznetsov (1967) and Razowski (1976). To describe head capsule structure and coloration in detail it was necessary to construct a new nomenclature of head horns, as no previous nomenclature existed. An attempt was made to use a terminology consistent with head capsule setal homology (Hinton, 1946) so as to permit phylogenetic analysis among caterpillars with

homologous head capsule structure. This nomenclature (Fig. 1) was developed for use in the description of *A. idyja argus* (Friedlander, 1986a) and for use as a model for all apaturine nymphalids.

Terminology used in describing features of the wings of adult butterflies is illustrated in Figure 2.

## CHARACTERS:

Characters used in this revision were compiled through detailed investigations of morphology, behavior and distribution of hackberry butterflies and their closest relatives. Most characters investigated in this study involved external cuticular structures examined by light and scanning electron microscopy. These were supplemented by life history and behavioral characters.

Representative specimens were disarticulated for morphological study, the procedures varying with the life stages involved. Specimens prepared for scanning electron microscopy (15-2000X) were air-dried or critical-point-dried and metal-coated for observation.

Study of adult morphology was carried out as proposed by Ehrlich (1958) and Sorensen (1980). Wing scale pigmentation patterns were investigated within the framework of Nijhout's (1978) model of developmental foci.

Rearing of individual specimens was conducted under standard conditions in the laboratory, as described in Friedlander (1986a). Eggs were kept in small, sealed plastic cups with leaves and a piece of paper toweling until larval eclosion. Larvae were reared in sealed plastic

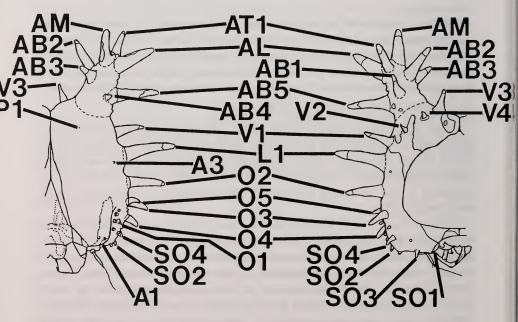


Fig. 1. Nomenclature of larval head horns (scoli).

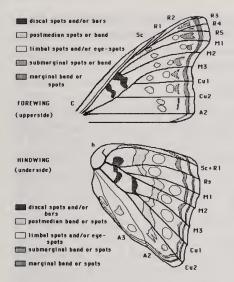


Fig. 2. Nomenclature of adult wing features (veins and markings).

bags. Fresh cuttings of suitable host plant material were provided daily or as needed. Humidity was kept high and was regulated by paper toweling, which was changed when the food was changed. Newly formed pupae were removed from rearing bags and suspended in open air cages so as to prevent damage by larvae and mold.

Behavioral data constitute an important source of characters which can best be recorded through observation in the field. Such data have previously not been applied to hackberry butterfly classification. Preliminary studies had indicated that larval and adult feeding behavior, and adult male courtship and female oviposition behaviors constituted character complexes useful in describing and defining taxa. Mating behavior constitutes one set of data which is particularly difficult to obtain. Courtships are commonly observed. Even cross-taxa couplings do occur (Ehle, 1950; A. Lewis, T. Friedlander, pers. obs.), but the success of these matings and the viability of any offspring produced is almost impossible to determine in the field.

Under artificial laboratory conditions pairings can be achieved with a minimum of effort and expense. Sleeve cages placed over fresh cuttings of the host plant exposed to normal light, temperature and humidity regimes suffice to breed hackberry butterflies. Cross-taxa pairings under these conditions can give valuable information on pre- and postmating, potential isolating mechanisms. Combined with field data on local sympatry, cross-breeding data help indicate whether or not populations have achieved sufficient isolation between one another to warrant designating them as species relative to each other (Hafernik, 1982). A number of these crosses have been carried out, with widely varying results (see previous section on species concept in hackberry butterflies).

Distributional data include the range, dispersion and density in time characteristic of a given taxon. Correlations of such data with ecological or geological data promote hypotheses on evolutionary events leading to these observed distributional patterns.

## CLASSIFICATION PROCEDURES:

Cladistic methodology (Andersen, 1978; Ashlock, 1974; Duncan and Stuessy, 1984; Estabrook, 1972; Hennig, 1966; Jong, 1980; Kavanaugh, 1972; Kiriakoff, 1959; Lundberg 1972; Wiley, 1981) was employed to construct testable hypotheses of genealogical relationships among taxa. Trees so derived were then used to infer biogeographical hypotheses about the taxa and their associated communities (Andersen, 1978; Ashlock, 1974; Cracraft, 1975; Jong, 1979; Nelson, 1974; Wiley, 1980).

Character analysis involves a 4-step process. First, homologies of characters are hypothesized (character homologies) (Atz, 1970; Bock, 1969). Multi-state characters are then investigated at the appropriate levels of universality to determine, with some associated probability, the polarity of the character states (character phylogenies) (Crisci and Stuessy, 1980; Jong, 1980; Watrous and Wheeler, 1981). Among the ways in which polarity is determined, the method of out-group comparison was used most extensively in this revision. Third, the distribution of shared, derived character states with regard to the taxa is then studied. The assignment of probabilities of their being uniquely derived is made to establish synapomorphies for tree construction (argumentation by character synapomorphies; parsimony applications). This is the basis of the cladistic method. Lastly, the correlation of synapomorphies with regard to taxa is investigated in light of the communities in which the taxa live in order to hypothesize biogeographical pathways (quasistatistical inference by character tracks) (Eldredge and Cracraft, 1980; Felsenstein, 1982).

In this study of hackberry butterflies I also looked at Wagner networks (Lundberg, 1972).

# Descriptions of Asterocampa Taxa

# Asterocampa J. Röber 1916

Doxocopa, C. Geyer, [1828] (part)

Doxocampa, A. Seitz, 1909 (lapsus calami)

 $Apatura,\,J.\,\,B.\,\,A.\,\,Boisduval\,\,and\,\,J.\,\,E.\,\,Le\,\,Conte,\,[1835]\,\,(part)$ 

Apartura, E. H. Ruffner, 1877 (part, misspelling)

Nymphalis, D. F. Poey, 1847 (part)

Chlorippe, S. H. Scudder, (1875) (part)

Chlorippus, W. T. Davis, 1924 (misspelling)

Asterocampa J. Röber, 1916; D. M. Bates, 1926 (Apatura celtis, type by subsequent designation)

[Celtiphaga W. Barnes and A. W. Lindsey, 1922 (Apatura celtis, type by original designation); excluded by Cowan (1970) from synonymy of Asterocampa by

reason of its being a junior objective synonym of Doxocopa Hübner through being a replacement name for Chlorippe Doubleday]

Apatura celtis Boisduval and Le Conte was designated the type species of Asterocampa by Bates in 1926.

The hackberry butterflies are recognized here as forming 2 major species groups, roughly corresponding to Skinner's (1911) Celtis and Clyton species groups, respectively.

The butterflies corresponding to Skinner's Clyton group are well defined. Eggs are tightly packed in clusters by ovipositing females. These eggs have a reduced aeropylar network. Larvae feed gregariously from emergence through middle instars. Pupae have blunt head prolongations. Adults are lacking dark limbal spots on the forewings.

The butterflies corresponding to Skinner's Celtis group have fewer defining characters. They are defined in the egg stage by chorionic reticulations, in the larval stage by the reduction of the head scolus AB5 in relation to L1, and in the adult by the reduction of certain genitalic structures (length of saccus and aedeagus in male genitalia, length of ductus in female genitalia).

EGGS: The eggs of hackberry butterflies (figured in: Comstock, 1953, 1961; Edwards, 1884b, 1897; Langlois and Langlois, 1964; Pyle, 1981, 1985; Riley, 1874; Scott, 1986) are roughly spherical with a diameter of slightly less than 1 mm each, and with a flattened base and slightly flattened micropylar region. Each has from 16 to 24 slightly prominent, longitudinal (vertical), flattened ribs, which are periodically punctuated with aeropylar holes. Between adjacent ribs are fine, closely spaced, horizontal costulae which form ladder-like rows. The top of the egg is sculptured with concentric rings of polygons bounded by minute ridges. The central half dozen or more polygons form the rosette around the micropyle.

The whitish eggs are glued to the substrate with a clear mucilage which holds them in position. Eggs are usually deposited on the undersides of leaves, although females in some populations of hackberry butterflies are known to place them on uppersides preferentially, or on nearby twigs, branches or epiphytes.

Two strategies among hackberry butterflies are evidently used in oviposition. The Celtis group of taxa deposits relatively small numbers of eggs in a clutch (1-50), usually in one layer and not in a tightly packed cluster. These butterflies generally select growth points on their larval host plant as sites for oviposition. This provides early instar larvae with the newest leaves.

Females belonging to the remainder of taxa deposite eggs in larger clutches (50-500) of multilayered masses of tightly packed eggs. They place their egg masses on leaves at the ends of branches at the edges of canopies in partial sunlight. The selected host plants are generally mature trees occurring in groves.

#### LARVAE:

Asterocampa larvae (figured in: Boisduval and Le Conte, 1829-1833[-1837]; Comstock, 1953, 1961; Edwards, 1884b, 1897; Langlois and Langlois, 1964; Mitchell and Zim, 1964; Peterson, 1962; Pyle, 1981, 1985; Riley, 1874; Scott 1986) are fusiform and without body scoli. The body tapers anteriorly towards the laterally expanded head capsule and posteriorly towards 2 short anal horns, much like satyrine caterpillars. The head capsule bears a single, branched horn (antler) at each of the dorsolateral corners and a frill of unbranched horns along the occiput. The many body setae are borne on chalazae. Larvae are variously green and have green or brown heads marked with white. The body is striped with lines or crenations of white to yellow and is studded with the minute whitish chalazae. Overwintering larvae lose their green color and appear mottled brown to reddish brown, turning green again in the spring with resumed feeding.

Hackberry butterflies typically have 5 larval instars (Comstock, 1953; Edwards, 1884b, 1897; Riley, 1874; Friedlander, pers. obs.). The third instar is the stage that diapauses over winter (e.g., Stamp, 1983), similar to most other apaturine nymphalids (Friedrich, 1977; Osanai and Arai, 1962a, b; Shiotsu, 1977; pers. obs.).

Scott (1981a) stated that "the hibernating generation of Asterocampa has six instars, versus 5 for the summer generation," attributing the extra instar to a specialization for winter survival. Edwards (1882) reported six larval instars for a small percentage of individuals of the overwintering generation of one species and stated (1884c) that A. clyton and A. celtis hibernated after the third molt. In his other papers he asserted that they hibernated after the second instar. Riley (1873, 1874) remarked that larvae diapaused after passing through the second or third molt but that there were only 5 instars. He introduced the idea that the number of instars might be different for the spring and fall generations of A. clyton and A. celtis. This has not been confirmed anywhere in the literature or by personal observation (routinely only 5). Some variability in excess of 5 instars has been observed in laboratory colonies and in related genera of butterflies (e.g., Friedrich, 1977).

Larvae of the Clyton group of hackberry butterflies are intensely gregarious as early instars, feeding and resting together in large numbers on leaves. When disturbed, they relocate and reaggregate. Even as mature larvae they can be found resting side by side. Larvae of the Celtis group of Skinner, while often found together as early instars, are far less gregarious.

## PUPAE:

Asterocampa pupae (figured in: Boisduval and Le Conte, 1829-1833[-1837]; Comstock, 1953, 1961; Edwards, 1884a, 1897; Langlois and Langlois, 1964; Mitchell and Zim, 1964; Mosher, 1916; Pyle, 1981, 1985; Riley, 1874; Scott, 1986) are attached to silken pads woven across the undersides of leaves (by corresponding mature larvae) by large crema-

sters in such a way as to hold them parallel to the leaf blades (except in *A. leilia*). The head is produced slightly into 2 horns extending beyond the eyes. The abdomen is arched and keeled dorsally, raised behind the thorax, and is laterally compressed. Pupae are also variously green and marked with whitish dots and dashes and blend in color and pattern with the leaves to which they are attached.

## ADULTS:

The hackberry butterflies are medium-sized Nearctic apaturine nymphaloid butterflies. They are somewhat sexually dimorphic in size and wing shape. The males are smaller and have narrower wings. Males are most commonly encountered during their courtship, either perching on sunlit tips of branches or tree trunks or aggressively pursuing passers-by. Females are usually found in search of suitable host plants but can as often be found sunning. Both sexes are encountered at sources of adult food, such as rotting fruit.

The hindwings are always patterned with a row of submarginal dark brown spots (limbal spots) and white and brown spots usually occur on the forewings. The dark spots of the uppersides of the wings are repeated below to form eyespots with pupils. The ground color of the wings spans browns and oranges ranging from light tan to dark black. The antennae always have light-colored tips. The blue iridescence common to the Neotropical apaturine Doxocopa and the Palearctic Apatura is not found in Asterocampa. Structural colors occur but are ruddy and blend in with the pigments of the wings.

The genus *Asterocampa* is defined relative to other apaturine nymphaloid butterflies by its genitalia and geographic distribution. It shares with *Chitoria* larval head capsule scolar arrangement and pupal cremastral design, features which are not yet known to be shared with any other genera. Genitalia of both sexes are quite similar between *Chitoria* and *Asterocampa*. The males have a reduced gnathos and females have paired signa on the bursa. These characters have not yet been determined to be synapomorphic.

## PARASITES AND PREDATORS:

The insect parasites and predators of hackberry butterflies have been reported for collections made by me through 1982 (Friedlander, 1984). The majority of these records are for individuals of the Clyton group, probably as a result of sampling frequency but possibly also as a result of the higher local density of individuals in populations of this species group.

Typical parasites of the egg stage across the genus are scelionids (Hymenoptera, Scelionidae) of the genus *Telenomus*. Their parasitism could possibly have (have had?) an effect on the egg mass design of Clyton group hackberry butterflies (Friedlander, 1986b). Trichogrammatid wasps have been found (2 per egg), but in only one collection of eggs (Celtis group).

Both hymenopterous and dipterous parasites have been reared from

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hackberry butterfly larvae (Diptera: Tachinidae; Hymenoptera: Braconidae, Eulophidae, Ichneumonidae). Middle instar larvae are generally attacked. All instars are attacked by both hemipteran and hymenopteran predators (Hemiptera: Pentatomidae, Reduviidae; Hymenoptera: Vespidae). With the dramatic increase in fire ant populations (Solenopsis invicta Buren, primarily) from Texas to Florida and northward, it is to be expected that these ants will cause heavy mortality of immature stages of hackberry butterflies across the Gulf states. Even emerging adults have been observed to be attacked by these noxious pests.

Chalcidid and ichneumonid wasps have been reared from pupae. The former is probably a primary parasite of pupae and the latter probably a larval-pupal parasite.

Adult butterflies have been observed to be attacked by both birds (sparrows) and lizards (anoles). They are often fed upon by spiders (crab spiders, house spiders, jumping spiders, orb-weavers). Occasionally a large dragonfly will take one on the wing.

## ADULT BEHAVIOR:

Various aspects of adult hackberry butterfly behavior have been reviewed recently. Scott (1975, 1982 (1983)) looked at mate-locating behavior and concluded that at least 2 species of *Asterocampa* were perchers, that is, the "males rest at characteristic sites and investigate passing objects by flying out at them to search for females." The short wings and thick bodies of males could very well be morphological adaptations to such behavior, as Scott suggests. Only one hackberry butterfly has been found to hill-top. This is *A. idyja argus* in Sonora, Mexico (D. Mullins, pers. comm.). Species of hackberry butterflies have been interpreted as being good examples for a resource-, or possibly also, female-defense polygyny mating system (Rutowski, 1984), males by their selection of perch sites monopolizing the larval host plants sought by females. This would be especially important if not only virgin females were most likely to be encountered at these sites, but also mated females capable of being mated gain.

Multiple mating does occur in *Asterocampa* (pers. obs. in field and in dissections) and males also "plug" females with a sort of sphragus, indicating that there could be an advantage for males to mate with previously mated females. Females could also benefit from multiple mating if some sort of nutrition is derived from matings.

Adult feeding behavior has been summarized by Neck (1983). Adults are attracted to a wide variety of nitrogen-rich food sources, including certain flowers.

Hackberry butterflies are for some reason often attracted to lights at night (Murtfeldt, 1884; Kendall and Glick, 1971 (1973)).

## ECONOMIC IMPORTANCE:

There is very little economic literature concerning hackberry butterflies. They are occasionally recorded as pests of hackberry trees (e.g., Dodge and Rickett, 1943; Herrick, 1935) but only rarely do they cause extensive defoliation (Langlois and Langlois, 1964; Solomon *et al.*, 1975). It is interesting to note that in both cases of defoliation mentioned above, the hackberry butterfly species was *A. celtis* inhabiting an island. Both *A. celtis* and *A. clyton* are periodically very abundant across the southeastern United States where their host plants are common (Riley, 1888; Israel, 1982).

# Asterocampa celtis (J. B. A. Boisduval and J. E. Le Conte, [1835]) (Genitalia, Figure 3)

Synonymies and discussion of types

Asterocampa celtis celtis (J. B. A. Boisduval and J. E. Le Conte, [1835])

?Papilio lycaon J. C. Fabricius, 1793 (identity obscure; junior homonym of Papilio lycaon Kühn, 1774)

Apatura celtis J. B. A. Biosduval and J. E. Le Conte, [1835] (biology); H. Lucas in R. de la Sagra, (1857) (Cuba!); W. H. Edwards, 1872 (biology), 1875 (biology), 1884 (biology); C. V. Riley, et al., 1888 (biology); H. Edwards, 1889 (biology) Apatura celtis aberration alb. H. Strecker, 1878 (abbreviated name, excluded

name)

Apatura celtis alba W. G. Wright, 1905 (change of status)

Apatura alicia W. H. Edwards, 1868 (revised status)

Apatura celtis variety alicia, H. Strecker, 1878

Apatura herse, A. G. Butler, 1874

Apatura lycaon, A. G. Butler, 1874; C. V. Riley, 1874 (biology); M. E. Murtfeldt, 1884 (biology)

Doxocopa lycaon, S. H. Scudder, 1872

Doxocopa celtis, S. H. Scudder, 1889

Chlorippe celtis, S. H. Scudder, 1889; J. W. Tutt, 1906 (biology)

Chlorippus celtis, W. T. Davis, 1924 (misspelling)

Chlorippe celtis variety alicia, H. Skinner, 1911

Chlorippe celtis aberration inornata R. H. Wolcott, 1916 (excluded name)

Asterocampa celtis, J. Röber, 1916; W. Barnes and A. W. Lindsey, 1922 (designation of type for Celtiphaga); D. M. Bates, 1926 (designation of type for Asterocampa); W. J. Holland, 1931; J. McDunnough, 1938; H. Stichel, 1938; C. B. Williams, 1949 (biology); G. Ehle, 1950 (biology); A. B. Kots, 1951; D. L. Bauer, 1953 (biology); K. Maeki and C. L. Remington, 1960 (karyotype); P. R. Ehrlich and A. H. Ehrlich, 1961; C. F. dos Passos, 1964; T. H. Langlois and H. H. Langlois, 1964 (biology); R. Heitzman, 1965 (biology); W. H. Howe, 1975; J. D. Solomon, et al., 1975 (biology); J. A. Scott, 1975 (biology), 1979 (1981) (biology); L. D. Miller and F. M. Brown, 1981, 1983; R. M. Pyle, 1981; P. A. Opler and G. O. Krizek, 1984 (biology)

Asterocampa celtis aberration alb, J. McDunnough, 1938 (misspelling, excluded name)

Asterocampa celtis form alb, L. D. Miller and F. M. Brown, 1981 (misspelling, excluded name)

Asterocampa celtis aberration inornata, J. McDunnough, 1938; L. D. Miller and F. M. Brown, 1981 (excluded name)

Asterocampa alicia, J. Röber, 1916; W. H. Howe, 1975 (part); L. D. Miller and F. M. Brown, 1981; R. M. Pyle, 1981 (part)

Asterocampa celtis alicia, J. McDunnough, 1938; W. D. Field, 1940 (possible partial misidentification); A. B. Klots, 1951 (part); C. F. dos Passos, 1964 Asterocampa clyton, R. M. Pyle, 1981 (probable misidentification, part: p. [49],

fig. 12)

Celtiphaga celtis, W. Barnes and F. H. Benjamin, 1926

Celtiphaga celtis aberration inornata, W. Barnes and F. H. Benjamin, 1926 (excluded name)

Celtiphaga celtis aberration alb, W. Barnes and F. H. Benjamin, 1926 (misspelling, excluded name)

Celtiphaga celtis alicia, W. Barnes and F. H. Benjamin, 1926

This taxon was based on a color drawing and life history notes supplied to Le Conte by John Abbot of Georgia in 1813[-1836] (Rogers-Price, 1983). Abbot considered the butterfly rare in swamps occurring near his home (Scudder, 1872b) in Screven County, Georgia. The figures of the adult are to be considered as representing the type. The description of this species, and thus the nominate subspecies, is considered to be complete in [1835] with the publication of the plate (Cowan, 1970). The whole description of *Apatura celtis* was complete in [1837].

Apatura alicia Edwards is based on 2 female specimens supplied to W. H. Edwards by E. Norton from the vicinity of New Orleans. Neither specimen could be located in Edwards' collection or elsewhere and so the beautiful and accurate figures published by him in the original description serve to represent the types. This taxon is considered here to be a subjective synonym of A. celtis celtis. It is a Gulf coast population of A. celtis celtis showing some differentiation but blending by degrees inland. The name has long been mistakenly used for populations of A. celtis in peninsular Florida (e.g., Edwards, 1880a-c) but must remain tied to butterflies of Louisiana and neighboring states. As a result, much of the argumentation as to its distinctness has been misapplied.

Apatura celtis alba Wright became available for synonymy in 1905, and is a name given to a color form of Asterocampa celtis celtis. The type is represented in W. H. Edwards (1875), figure 5 of Apatura celtis. By implication its type locality is Coalburgh, West Virginia.

# Asterocampa celtis reinthali, New Subspecies

?Papilio lycaon J. C. Fabricius, 1793 (identity obscure; junior homonym of Papilio lycaon Kühn, 1774)

Apatura alicia, W. H. Edwards, 1880 (biology); H. Edwards, 1889 (biology) Chlorippe alicia, W. J. Holland, 1898

Asterocampa alicia, W. J. Holland, 1931; W. H. Howe, 1975 (part); R. M. Pyle, 1981 (part); P. A. Opler and G. O. Krizek, 1984 (clinal subspecies?)

Asterocampa celtis alicia, W. M. Davidson, 1958 (biology); A. B. Klots, 1951 (part)

This taxon, named after the late Dr. Walfried J. Reinthal, has previously been included under the name *Asterocampa alicia*. Like *A. alicia*, it is a large, coastal *A. celtis*. The male type is selected from specimens taken in April at Ocoee, Florida ("A. alicia, 4-5-39. Ocoee, Fla." "collected by, Mrs. C. N. Grimshawe, Miami, Florida"). The female allotype ("A. alicia, 4-7-49, Ocoee, Fla" "collected by, Mrs. C. N. Grimshawe, Miami, Florida") will be deposited with the holotype at the Carnegie Museum of Natural History.

The types are selected from a series of specimens set aside by Dr. Reinthal in his own collection. The remaining 10 specimens in this series are designated paratypes. All will be deposited in the Carnegie Museum of Natural History.

Paratype males (5): "Largo, Fla, VII-11 '49, F. H. C." "W. J. R."; "Port Orange, Fla. 7-17-48" "A. celtis alicia [male]" "W. J. R."; "FLA: Orange Co., Ocoee. 11-12.vi.1954, J. Bauer, C. M. Acc. 17023" "21.vi." "W. J. R.", 16.VII.49, Largo, Fla, F. H. C."; "13.IV.57, Oviedo, Fla, [male] alicia" "Genit. prepar., No 17 1959, W. J. Reinthal" [no head, no abdomen].

Paratype females (5): "Lk. Okeechobee, Fla. VII-21-1940" "F. H. Chermock, Coll." "W. J. R." [no abdomen]; "Fla. St. Johns Co., Summer Haven 16 mi., St. Augustine, E. P. Mellon II 3 VIII 1953" "W. J. R."; "19.VIII.37, Ocoee, Fla, A. alicia"; "16.VII.49, Largo, Fla, F. H. C." [no head, no abdomen]; "5.VIII.56, Oviedo, Seminole Co., Fla." "Genit. prepar., No 18 1959, W. J. Reinthal" [no head, no abdomen].

# Asterocampa celtis antonia (W. H. Edwards, [1878])

Apatura antonia W. H. Edwards, 1877 [1878]; F. M. Brown, 1967 (lectotype, type locality)

Apatura celtis variety antonia, H. Strecker, 1878

Apatura celtis variety antonio, J. B. Smith, (1884) (misspelling)

Apatura celtis, E. M. Aaron and S. F. Aaron, (1885) (part)

Apartura celtis, E. H. Ruffner, 1877 (part, misspelling)

Apatura antonia variety montis W. H. Edwards, 1883; W. G. Wright, 1905, C. J. Maynard, 1891 (revised status)

Apatura montis, W. G. Wright, 1905; B. N. Schwanwitsch, 1924 (morphology); F. M. Brown, 1967 (lectotype)

Chlorippe antonia, W. J. Holland, 1898

Chlorippe montis, W. J. Holland, 1898

Chlorippe leilia, W. J. Holland, 1898 (misidentification)

Chlorippe antonia montis H. G. Dyar, [1903]

Chlorippe celtis variety antonia, H. Skinner, 1911

Chlorippe celtis variety montis, H. Skinner, 1911; V. F. Calkins, 1932

Doxocopa celtis, F. D. Godman, (1901) (part)

Doxocopa antonio, K. R. Coolidge, 1911 (misspelling)

Doxocopa montis, K. R. Coolidge, 1911

Doxocopa leilia, K. R. Coolidge, 1911

Asterocampa leilia antonia, J. Röber, 1916; H. Stichel, 1938

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Asterocampa leilia, W. J. Holland, 1931 (misidentification); J. S. Garth, 1950 (misidentification); R. M. Pyle, 1981 (misidentification, part: p. [284]); P. M. Montgomery, 1984 (misidentification: p. 4)

Asterocampa celtis antonia, J. McDunnough, 1938; A. B. Klots, 1951; C. F. dos

Passos, 1964; K. S. Brown, Jr., 1965

Asterocampa celtis montis, J. Röber, 1916; J. McDunnough, 1938; H. Stichel, 1938; A. B. Klots, 1951; C. F. dos Passos, 1964

Asterocampa celtis, C. C. Hoffmann, 1940 (part); P. R. Ehrlich and A. H. Ehrlich, 1961 (part); J. A. Scott and G. R. Scott, (1980) (part, biology); R. M. Pyle, 1981 (misidentification, part: p. [285])

Asterocampa antonia, W. J. Holland, 1931; W. J. Reinthal, 1966 (biology); W. H. Howe, 1975; L. D. Miller and F. M. Brown, 1981, 1983; R. M. Pyle, 1981

Asterocampa antonio, E. R. Tinkham, 1944 (misspelling)

Asterocampa montis, W. J. Holland, 1931; W. H. Howe, 1975; L. D. Miller and F. M. Brown, 1981, 1983; R. M. Pyle, 1981

Asterocampa subpallida, J. A. Comstock, 1953 (possible misidentification, part: p. 134)

Celtiphaga celtis antonia, W. Barnes and F. H. Benjamin, 1926 Celtiphaga celtis montis, W. Barnes and F. H. Benjamin, 1926

Apatura antonia Edwards (1877 [1878]) was described from a series of specimens taken in Texas by J. Boll and G. W. Belfrage of Texas (and a collector in Arizona, possibly Dr. Charles Smart (Brown, 1967)). The type locality is restricted by F. M. Brown (1967) and a lectotype was designated by him and W. J. Reinthal in the same article. The type and paratypes have been examined and are in the Carnegie Museum of Natural History.

Edwards (1883) characterized A. antonia variety montis after receiving a series of specimens collected by H. K. Morrison from Arizona. He compared these with his collection of A. antonia-like specimens which included specimens from J. Doll (Arizona, etc?) and E. A. Dodge (Colorado). Brown (1967) selected the lectotype, which together with paratypes are deposited in the Carnegie Museum of Natural History. These also have been examined.

A good discussion of Edwards' type material is found in Brown (1967).

# Diagnoses of taxa

A. celtis is a member of the Celtis group. Virtually all larvae of A. celtis celtis lack the antler scoli AB5. Adults are best distinguished by the single, large unpupilled eyespot of the forewing (Cu1). Limbal spot M3 above it is usually small and may be ringed posterobasally with dark brown and orange. It is virtually impossible to separate individuals of A. celtis antonia and A. celtis celtis in hybrid zones. As a rule of thumb, specimens with equal-sized spots M3 and Cu1 can be assigned to A. celtis celtis if the former spot is entirely white. Populations exhibiting intermediate coloration and pattern extend from northwestern Nebraska to central Texas. Similar difficulties are encountered in

separating A. celtis celtis from A. celtis reinthali in zones of presumed hybridization in northern Florida and coastal Georgia and South Carolina.

The whitish yellow larval markings of *A. celtis reinthali* are much more yellow than in *A. celtis celtis*. The supraspiracular markings tend to be obscure rather than to form a crenated line. Mature larvae are known to have well developed antler scoli AB5 like those found in *A. celtis antonia*, but which are virtually absent in *A. celtis celtis*. Adult *A. celtis reinthali* are considerably larger than the nominate subspecies, and have a brighter ground color above and larger, lighter blue pupils in the ocelli. The pupils of Cu1 in the FW above are lateral (off-center) and the limbal spots M1 of the HW are asymmetrical, each being drawn out into a point distally, and their pupils with scales dividing in 2 tracks outwardly. The butterflies are peninsular Floridian in origin. They differ from true *A. alicia* (here, *A. celtis celtis* form "alicia") not so much in size but in coloration and pattern. True *A. alicia* is darker in ground color (grayish brown), the pupils of eyespots are smaller, and limbal spots Rs of the HW are not drawn out into points laterally.

A. celtis antonia is more western than the other two and differs from them in the adult stage by retaining eyespots in the FW. These limbal spots are not generally expressed in the other subspecies. The host plant most commonly used is *Celtis reticulata* Torrey. Larvae differ by retaining all the antler scoli AB5 commonly being lost in the eastern subspecies.

# Descriptions of life stages

Immature stages of *A. celtis celtis* were described in detail by Riley (1874), Edwards (1875, 1880c, 1884b) and Scudder (1889). Those of *A. celtis reinthali* were described in detail by Edwards (1880c). Immature stages of *A. celtis antonia* are described here for first time. Pyle (1984) describes the rearing of this species in Colorado in his popular account of butterfly natural history. Scott (1986) illustrates eggs of *A. celtis celtis* in an excellent color photograph (Pl.1, [fig.] 140). Pyle (1981, 1985) photographically illustrates the mature larva and pupa of *A. celtis celtis* (Pl. 45R, 45L).

#### EGGS AND EGG DEPOSITION:

Eggs of *A. celtis celtis* finely sculptured with reticulations between costae, except in micropylar region, 16-21 ribs; 0.7-0.9 mm wide, 0.9 mm high. Micropylar rosette with 9 petals.

Light yellow eggs of A. celtis reinthali deposited in small clusters on undersides of leaves or on branches and epiphytes on larval host plant Celtis laevigata Willd. Other details of egg morphology expected to be quite similar to those of A. celtis celtis. Edwards (1880c) reported pale yellow-green eggs having 20 vertical ribs.

Eggs of *A. celtis antonia* finely sculptured, slightly reticulated between costae, with 17-24 ribs; those from southeastern part of range with fewer ribs than those

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from far western limits. Dimensions 0.8-0.1 mm wide, 0.8-1 mm high. Micropylar rosette with 11-14 petals.

#### LARVAE:

First instar head capsule of *A. celtis celtis* very dark brown, with 5 pairs of scoli developed, scoli almost twice size of simple eye; 0.63-0.74 mm wide. Body length about 3.5 mm. Head and proleg setae unbranched; body setae extremely short-branched. Crampets (Pl.17, fig. C; defined in: Friedlander, 1986a) present on prolegs. Mandibles with teeth. Body light green. Anal horns about 0.1 mm long each, light brown. First instar larval head capsule of *A. celtis reinthali* dark brown. Body green; total length about 2 mm. First instar larva of *A. celtis antonia* with dark brown head capsule, scoli twice width of simple eye. Anal horns developed.

Second instar larva of *A. celtis celtis* with long scoli, antlers somewhat lateralized (diverging at nearly a right angle), AB5 absent. Head capsule very dark brown. Scoli V2 absent. Whitish body markings obvious in this stage. Anal horns green, variably sclerotized. Head capsules of second instar larva of *A. celtis reinthali* very dark brown, rarely green with brown antlers, AB5 absent, antlers lateralized. Body green with whitish lines and crenations as in mature larva. Total length about 3.5 mm. Head capsule of second instar larva of *A. celtis antonia* mostly dark brown. Scoli AL spine-like, antler base less than mandibular width, AB5 about half as long as L1. Scoli V2 absent, Anal horns tan.

Third instar head capsule of A. celtis celtis mostly dark brown. Body coloration as in second instar. Third instar larva of A. celtis reinthali with variably dark brown to mottled head capsule, with somewhat lateralized antlers. Body green with markings as before; total length about 7.5 mm. Third instar larva of A. celtis antonia with mostly dark brown head capsule. Diapausing larvae with reduced antlers (shorter with less well developed scoli), body with mixed gray, brown and pink.

Fourth instar of *A. celtis celtis* with head capsules mostly brown. Body markings same as mature larva. Fourth instar larva of *A. celtis reinthali* also with head capsule variably brown. AB5 small to vestigial. Body same as third instar, except heart-line spots apparent. Total length about 14 mm. Fourth and fifth instar larvae of *A. celtis antonia* in 2 color morphs with regard to head capsule: brown (brown striped; most of head capsule dark brown); green (at extreme, only antlers brown).

Fifth instar larva of *A. celtis celtis* green. Head capsule either green or dark brown with lateral whitish streaks, antlers always with black tips. Heart-line with yellowish white spots anteriorly on abdominal segments, broadened into chevrons into inner subdorsal band region. Dorsolateral stripe yellowish white. Crenated line of yellowish white in supraspiracular area, sometimes broken into dashes. Subspiracular stripe whitish. Anal horns long. Total length about 30 mm

Fifth instar larva of *A. celtis reinthali* green, with variably colored head capsule, green to dark reddish brown, with whitish vertical stripes laterally, and black-tipped antlers. Heart-line marked with small yellow spots. Dorsolateral and subspiracular stripes yellowish. Supraspiracular area marked with diagonal dashes of yellowish white, higher ends posteriorly. Anal horns long. Body markings somewhat obscure compared to earlier instars. Length of males about 29 mm, females, 36 mm.

Fifth instar larval head capsule of *A. celtis antonia* with long antlers, 1.7 mm, not including terminal scoli. AL and AM subequal, of moderate length, slightly smaller than AB2 and AB5. AB1, AT1, AB3 and AB4 (in order) even smaller. L1 longest of head scoli, 0.9 mm, followed by O2, V1, V3 and O3. Ratio of AB5 to L1 approximately 0.6. Head capsule 3.2 mm high, excluding mandibles. Mandible with one notch in incisor. Body color green. Heart-line with yellowish white spots anteriorly on middle abdominal segments; lacking in form called here "mexicana" (see: adult description). Dorsolateral stripe yellowish white to light yellow, somewhat wavy in some populations. Subdorsolateral and supraspiracular areas with diagonal yellowish white dashes, posterior ends higher, connecting with posterior vertical bar, almost connected below bar by chalazae to form crenated line (with ascending bars); obscure in "mexicana." Subspiracular stripe yellowish white. Shade of green and amount of yellowish in both body color and in stripes varies.

## PUPAE:

Pupa of A celtis celtis 19-25 mm long, about 8-9 mm high at abdominal crest maximum. Head prolongations elongate, pointed. Body light green, finely speckled with light yellow or whitish dots, marked with yellowish white along dorsal crest, wing veins and wings' edges posteriorly. Supraspiracular transverse dashes present; subspiracular line an extension of one along the outer wing margin, almost forming an undulating line. Crest finely serrate, with blunt spines anteriorly on each segment subtended by pair of small black spots. Pupal cremaster length 2.3-2.8 mm. Length of pupa of A. celtis reinthali 23-25 mm, width about 8 mm, maximum height about 10 mm. Head prolongations prominent, pointed. Body yellowish green, speckled with yellowish white dots, marked with pale yellow and whitish streaks. Streaks along dorsal crest from head prolongations, merging on thorax; also posteriorly down serrated abdominal portion. Both wing veins and posterior wing edges so marked. Indications of supraspiracular transverse dashes present. Abdominal crest with blunt spines anteriorly on each segment subtended by pair of small black dots. Pupa with cremastral length of 2.5-2.9 mm. Pupa of A. celtis antonia green, usually speckled with white, with whitish markings along dorsal crest, wing veins and margins, and in diagonal streaks on sides of abdomen. Length 17-21 mm, height at crest maximum 6.5-9.0 mm. Head prolongations sharp. Some development of eye spines, as in A. leilia, as best seen in form "mexicana." Abdominal crest finely serrate, anterior margins of segments blunt-spined with subtending small black dots, one on each side. Subspiracular line on abdomen usually present. Pupal cremaster length 2.3-2.8 mm. Pupal cases with greenish cast after emergence, whitish markings apparent.

## ADULTS:

Antennae of *Asterocampa celtis celtis* (Pl.20, figs. A-C) dark brown, finely ringed with lighter brown on flagellar segments giving faintly dotted appearance; apical portions slightly swollen, dark brown with bare pale yellow (tan with aging of preserved specimens) tips. Palps, general body scaling and ground color of wings above, grayish brown and yellow orange mixed. Forewing costal length (Figure 4) of *A. celtis celtis* 20.0-28.5 mm (males, 24.0  $\pm$  1.6 mm, n = 248), 22.0-32.5 mm (females, 27.3  $\pm$  1.8 mm, n = 151); larger, coastal form "alicia" accounts for most of high values in both sexes. Male genitalia: saccus 2.2-

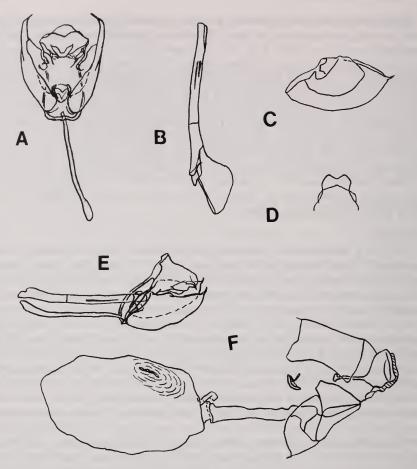


Fig. 3. Genitalia of Asterocampa celtis (B. & L.). Male genitalia

Whole genitalia (A, ventral view, valves spread) with aedeagus (B) separate: Texas: Travis Co., Austin, September 1977, t. Friedlander. TF gen. prep. no. 1977. A. celtis antonia (Edwards).

Right valve (C, mesal view) and uncus (D, ventral view): Louisiana, no date, CMNH. TF gen. prep. no. 1982-30. A. celtis celtis.

Whole genitalia (**E**, left lateral view): Texas: Travis Co., Austin, September 1977, T. Friedlander. TF gen. prep. no. 1977. *A. celtis antonia. Female genitalia*:

Whole genitalia (**F**, left lateral view): Texas: Travis Co., Austin, September 1977, T. Friedlander. TF gen. prep. no. 1977. *A. celtis antonia*.

2 6 mm, aedeagus 2.9-3.2 mm, valves 1.9-2.2 mm, uncus shallowly bifid, hairs of anal brush recurved. Female genitalia: ductus 1.7-2.4 mm, signa on elongate corpus 2 long longitudinal strips on right side. For a more complete description of this subspecies the reader should consult my dissertation.

Photographic figures of *A. celtis celtis* found in: Ebner, 1970 (p. 95, male, d, v); Harris, 1972 (Plate 6: fig. 1, male, d; fig. 2, female, d); Holland, 1898, 1931 (Plate

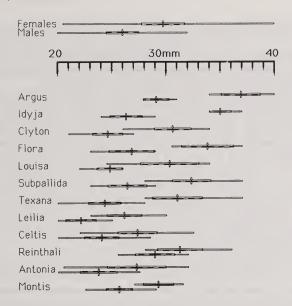


Fig. 4. Costal forewing measurements of hackberry butterflies, showing mean lengths, ranges and one standard deviation, given in millimeters.

XXIII: fig. 3, male, d; fig. 4, female, d; fig. 13, male, v); Milne and Milne, 1980 (Plate 604, male, d); Opler and Krizek, 1984 (Fig. 191, male, d; Fig. 192, male, v); Pyle, 1981 (Plate 664R, male, d); Pyle, 1985 (Plate 664L, male, v; Plate 664R, male, d); Scott, 1986 (Plate 22 [fig.] 140, female, d); Smart, 1977 (p. 210, fig. 8, male, d); Sutton and Sutton, 1985 (Plate 366, males, v.d); Williamson, 1979 (cover photograph. v); Wright, 1906 (Plate XXIII: fig. 245, female, d). Howe (1975) illustrated individual specimens (Plate 11: fig. 11, female, d; fig. 12, male, d; fig. 25, male, v).

A. celtis celtis dorsal FW limbal spots mostly white. Spot M1 usually white, but sometimes mostly white with dark brown basally. Spot Cu1 dark brown, usually larger than M1 and noticeably the largest limbal spot, surrounded by yellowish orange ring (more organe in "alicia"). Spot Cu2 sometimes faintly indicated by dark brown spot with blush of yellowish orange scaling anterobasally. Limbal spots of dorsal HW large (Sc+R1 to Cu2), dark brown in local field (merging rings) of yellow orange in orange.

Ventrally, FW limbal spots R5, M2 and M3 white. Spot M1 basally dark brown, apically white, ringed in light yellow (yellow more intense in "alicia"). Spot Cu1 large, dark brown, ringed in light yellow, without pupil. Limbal spots of ventral HW (Sc+R1 to A2) dark brown with whitish blue pupils, ringed in yellow in local brown ring in tan field. Spot A1 joined to Cu2 at inner dark brown scaling, or vestigial. Spot A2 without pupil and outward brown ring, usually small, oval.

Antennae of *Asterocampa celtis reinthali* (Pl.20, figs. D-F) like those of *A. celtis celtis*. Palps, general body scaling and ground color of wings above, grayish brown and burnt orange mixed. Costal lengths of forewings (Fig. 4) of *A. celtis reinthali*, 25.5-32 mm (males,  $28.9 \pm 1.8$  mm, n = 44), 28-36 mm (females,  $31.2 \pm 1.8$  mm, n = 44), n = 440.

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 $2.1\,\mathrm{mm},\,\mathrm{n}=26$ ). Male genitalia similar to *A. celtis celtis*: saccus 2.8-3.0 mm, aedeagus  $3.6\text{-}4.3\,\mathrm{mm},\,\mathrm{valves}\,2.0\text{-}2.5\,\mathrm{mm},\,\mathrm{uncus}\,\mathrm{shallowly}\,\mathrm{notched},\,\mathrm{dorsal}\,\mathrm{brush}\,\mathrm{with}\,\mathrm{upwardly}\,\mathrm{curved}\,\mathrm{hair}\text{-scales}.$  Female genitalia: ductus  $2.4\text{-}2.6\,\mathrm{mm},\,\mathrm{signa}\,2\,\mathrm{long}\,\mathrm{strips}\,\mathrm{on}\,\mathrm{right}\,\mathrm{side}\,\mathrm{of}\,\mathrm{elongate}\,\mathrm{bursa}.$  For a more complete description of this subspecies the reader should consult my dissertation.

Photographic illustration of adult of *A. celtis reinthali* found in: Harris, 1972 (Plate 6: fig. 3, male, d; fig. 4, female, d); Holland, 1898, 1931 (Plate XXIII: fig. 9, male, d; fig. 10, female, d); Lewis, 1973 (p. 13: fig. 6, male, d); Scott, 1986 (Plate 19 [fig.] 140d, male, d). Excellent drawings made by Howe (1975) of individual specimens (Plate 11: fig. 9, male, v; fig. 23, female, d; fig. 24, male, d).

A. celtis reinthali dorsal FW limbal spots mostly white. Spot M1 basally dark brown. Spot Cu1 noticeably the largest limbal spot, dark brown with small lateral pupil, surrounded by orange ring. Limbal spots of dorsal HW (Rs to Cu2), dark brown, sometimes with bluish white pupils, in orange field. Spot M1 usually elongated laterally. Limbal spots of HW dorsally in females in field of light yellow orange in larger field of orange.

Ventrally, FW limbal spots R5, M2 and M3 white. Spot M1 dark brown basally, white apically, ringed in yelllow. Spot Cu1 dark brown with yellow ring (orange brown at junction) with a few bluish white scales forming pupil. Limbal spots of ventral HW (Sc+R1 to Cu2) dark brown with large whitish blue pupils, ringed in strong yellow-orange in local dark brown field. Spot M1 asymmetrically elongate, pointed basally with scales of pupil merging distally. Spot A1 joined to Cu2, often vestigial. Spot A2 dark brown with strong yellow-orange ring, elongate.

Antennae of Asterocampa celtis antonia (Pl.20, figs, G-O) dark brown, finely ringed with lighter brown on flagellar segments giving decidedly dotted appearance; apical portions as before, except club relatively shorter. Palps, general body scaling and ground color of wings above, medium brown (more orange in some populations) and dark brown mixed. Postmedian spots of ventral HW prominent to obscure. Eastern forms with forewing costal length 20.0-27.5 mm (males,  $23.7 \pm 1.7$  mm, n = 182), 20.5-32.0 mm (females,  $27.2 \pm 2.7$  mm,  123). Form "mexicana", found in the lower Rio Grande valley of Texas and southward with small females, accounts for most low values. Western form "montis" slightly larger, 22.5-29.0 mm (males,  $25.6 \pm 1.2$  mm, n = 89), 27.0-31.5 mm (females,  $29.2 \pm 1.4$  mm, n = 16). Male genitalia: saccus 1.9-2.3 mm, aedeagus 2.5-3.0 mm, valves 1.5-1.9 mm. Uncus with shallow notch. Dorsal brush with upturned hair-scales. Female genitalia with short ductus (1.5-2.2 mm), bursa globular, often with 2 sclerotized signa, in longitudinal strips of right side. For a more complete description of this subspecies the reader should consult my dissertation.

Photographs of adult of *A. celtis antonia* published in sources: Brown, 1967 (Fig. 18, antonia, lectotype, male, d, v; Fig. 19, montis, lectotype, male, d, v); Ferris and Brown, 1981 (p. 356, antonia, male, d, v); Holland, 1898, 1931 (Plate XXIII: fig. 7, near antonia, male, d; fig. 8, near antonia, female, d; fig. 11, montis, male, d; fig. 12, antonia, male, d); Montgomery, 1984 (p. 4, "Empress Leilia...," male, d); Pyle, 1981 (Plate 662R, mexicana, female, d; Plate 663L, antonia, male, v; Plate 664L, antonia, male, v); Pyle, 1985 (Plate 663L, antonia, male, v; Plate 663R, mexicana, female, d); Scott, 1986 (Plate 19 [figs.] 140, male, d; 140b, female, d; 140c, male, v). Excellent figures of individual specimens found in Howe (1975: Plate 11: fig. 21, near antonia, female, d; fig. 22, near antonia, male,

d; Plate 12: fig. 11, antonia, male, d. v; fig. 12, antonia, female, d. v; Plate 13: fig. 6, montis, male, d, v; fig. 7, montis, female, d, v).

A. celtis antonia dorsal FW limbal spot R5 white, large. Spot M1 white with dark brown basal cup or, more typically, entirely very dark brown with white pupil, usually small. Spot M2 white, medium-sized, sometimes bordered anterobasally with dark brown. Spots M3 and Cu1, large, subequal in size, very dark brown with white pupils, ringed with light brown. Spot Cu1 in "montis" pupilled with bluish white scales, laterally. Rarely, spot Cu2 indicated by tiny, very dark brown spot. Limbal spots of dorsal HW large (Sc+R1 to Cu2), very dark brown, last few pupilled with bluish white to white, all in field of ground color, or, especially in females, in field of a more yellowish brown.

Ventrally, FW limbal spots M1, (rarely M2), M3, and Cu1 very dark brown with pupils of light blue to white, all surrounded by local field of yellow inside dark brown rings. Spot R5 sometimes expressed as eye-spot in males. Spot M2 most often white with border of dark brown and yellow anterobasally, but full range of expression occurs. Limbal spots of ventral HW (Sc+R1 to A2) very dark brown with whitish blue pupils, also surrounded by local field of yellow inside dark brown rings.

## Range

A. celtis celtis (Pl.1): Eastern United States and extreme southern Ontario, Canada. Specimens examined (over 1,500 non-reared adults; state localities given alphabetically by counties):

CANADA: Ontario (province)

U.S.A.: ALABAMA: Elmore, Greene, Jackson, Madison, Marengo, Mobile, Montgomery, Tuscaloosa; ARKANSAS: Desha, Faulkner, Hempstead, Jefferson, Pulaski, Sharp, Washington; COLORADO: Denver, Jefferson, Yuma; CONNECTICUT: Fairfield, Litchfield, New Haven, Tolland; FLORIDA: Leon, Liberty; GEORGIA: Bibb, Chattahoochee, Clarke, Decatur, De Kalb, Monroe, Walker; ILLINOIS: Adams, Cook, Logan, Macon, Madison, Mercer, Platt; INDIANA: Adams, Carroll, Jackson, Knox, Kosiusko, Marion, Vigo, Wabash; IOWA: Dallas, Fremont, Polk, Pottawattamie; KANSAS: Cherokee, Douglas, Franklin, Greenwood, Johnson, Labette, Shawnee, Sumner, Wyandotte; KENTUCKY: Jefferson; LOUISIANA: East Baton Rouge, Jefferson, Jefferson Davis, Rapides, Sabine, St. Charles, St. Landry, St. John The Baptist (parishes); MARYLAND: Allegany, Baltimore, Washington; MASSACHUSETTS: Hampshire; MICHIGAN: Washtenaw; MINNESOTA: Clay, Faribault, Hennepin, Ramsey; MISSISSIPPI: Clay, Grenada, Hancock, Hinds, Lee, Lowndes, Madison, Oktibbeha, Rankin, Simpson, Tallahatchie, Tippah, Warren, Wilkinson; MISSOURI: Clay, Cole, Jackson, Jasper, Laclede, Pike, St. Louis; NEBRASKA: Adams, Cherry, Douglas, Lancaster, Platte, Red Willow; NEW JERSEY: Bergen, Essex, Middlesex, Morris, Sussex; NEW YORK: Columbia, Greene, Richmond (Staten Island), Tompkins, Westchester; NORTH CAROLINA: Cabarrus, Durham, Halifax, Mecklenburg, Orange; OHIO: Erie, Franklin, Hamilton, Miami, Montgomery, Pike; OKLAHOMA: Cleveland, Cotton, Garfield, Mayes, Mc-Curtain, Murray, Oklahoma, Osage; PENNSYLVANIA: Allegheny, Beaver, Berks, Bucks, Franklin, Greene, Lancaster, Lycoming, Washington, Westmoreland; SOUTH CAROLINA: Calhoun, Charleston, Edgefield, Pickens, Richland; SOUTH DAKOTA: Brookings, Grant, Roberts; TENNESSEE: Anderson, Davidson, Giles, Knox, Madison, Marion, Maury, Polk, Sullivan, Wilson; TEXAS: Bastrop, Bowie, Brazos, Dallas, Denton, Harris, Harrison, Houston, Kaufman, Limestone, Tarrant, Travis, Van Zandt, Williamson; VIRGINIA: Bath, Essex, Fairfax, Fauquier, Loudoun, Montgomery, New Kent, Washington, Wise; WASHINGTON, D. C.; WEST VIRGINIA: Hampshire, Kanawha, Morgan; WISCONSIN: Oneida.

A specimen captured in Montreal, Quebec, Canada (Stevenson, 1899) is to be considered a stray and most probably was an importation.

A. celtis reinthali: Peninsular Florida, coastal Georgia and South Carolina. Specimens examined (over 350 non-reared adults):

U.S.A.: FLORIDA: Alachua, Brevard, Flagler, Hernando, Indian River, Nassau, Okeechobee, Orange, Palm Beach, Pinellas, Polk, Sarasota, St. Johns, Seminole, Volusia; GEORGIA: Camden, Chatham, Glynn, Liberty, McIntosh; SOUTH CAROLINA: Charleston, Jasper.

A. celtis antonia: Northern Mexico, southwestern United States: Arizona, western Colorado, western Kansas, western Nebraska, New Mexico, western Oklahoma, western Texas; rarely, southern California (San Bernardino County), southern Nevada and Utah; forming hybrid zone with A. celtis celtis from Texas to Nebraska. Specimens examined (over 1000 non-reared adults) [from "montis" (°) (over 250 non-reared adults)]:

MEXICO: Chihuahua, Hidalgo, Nuevo Leon, San Luis Potosi, Tamaulipas [states]

U.S.A.: ARIZONA°: Cochise, Coconino, Gila, Graham, Pima, Pinal, Santa Cruz, Yavapai; COLORADO: Boulder, Clear Creek, Denver, Douglas, Jefferson, Yuma; KANSAS: Shawnee, Summer; NEBRASKA: Dawes, Sioux; NEW MEXICO: Bernalillo, Catron°, Dona Ana°, Eddy, Grant°, Luna, Otero°, San Miguel, Sierra°, Socorro°, Union; OKLAHOMA: Blaine, Caddo, Catton, Garfield, Kiowa, Lawton, Woodward; TEXAS: Armstrong, Bailey, Baylor, Bee, Bell, Bexar, Blanco, Bosque, Brewster°, Brisco, Brooks, Caldwell, Calhoun, Cameron, Coleman, Collingsworth, Comal, Crockett, Dallas, Duval, Frio, Gillespie, Gonzales, Hall, Hays, Hidalgo, Jeff Davis°, Jones, Kenney, Kerr, Kleberg, Live Oak, Llano, Lubbock, Mason, McCulloch, McLennan, Medina, Mitchell, Nueces, Palo Pinto, Pecos, Presidio, Randall, San Patricio, Shackelford, Starr, Sterling, Sutton, Tarrant, Terrell, Tom Green, Travis, Val Verde, Webb, Wheeler, Wichita, Wilbarger; also, rarely: Bastrop, Caldwell, Coryell, Lee, Parker; UTAH°: Weber [dubious record], Washington; WYOMING: Laramie.

A. celtis antonia occurs in Garfield county, Utah (Callaghan and Tidwell, 1971 (1973)) and is expected to be found in 4 more of the southern counties (Gillette, 1983). Unpublished records are available for Grand, San Juan and Washington counties, Utah (Gilette, pers. comm.). Garth's (1950) record of A. leilia from the Grand Canyon (Arizona) is also this subspecies of A. celtis. John Emmel (in correspondence) gives one record of this butterfly from the San Bernardino Mts. in southern California, tentatively considered a stray.

#### Discussion

A. celtis celtis is a common woodland butterfly and is perhaps the best known of the hackberry butterflies. Its colonizing ability exceeds that of

A. clyton and it is to be expected to be found beyond the range of its host as a stray. It will probably be found extending its range northwestward towards Montana as hackberry trees are planted there as windbreaks.

A. celtis reinthali is the large A. celtis celtis-like butterfly of peninsular Florida and the southern Atlantic coast. This subspecies was long included under the name of A. alicia but the two have been known for the last 30 years to be different. It probably evolved through isolation in central Florida during the glacial maxima of the Pleistocene. It is currently hybridizing on both the Gulf and Atlantic coasts.

These butterflies are similar to *Papilio lycaon* Fabricius, which was based on a drawing of a butterfly from the collection of D. Drury. F.M. Brown (1965) has shown that butterflies in Drury's collection included those from the southeastern United States. It remains possible that *Papilio lycaon* Fabricius was a hackberry butterfly.

Lucas' (1857) record of *A. celtis* occurring in Cuba should be seriously considered. It is possible that this species could have been (or still could be) on the island. If so, I think that the subspecies in question would more likely have been (be) *A. celtis reinthali* than *A. celtis antonia*.

A. celtis antonia is often confused with A. leilia. Holland (1898, 1931) published a photograph of A. montis mistakenly under the name of A. leilia. This error was probably based on Hollands' relabelling of Edwards' collection. In addition, Holland mistakenly considered the type locality of A. montis to be Colorado and figured specimens from the Denver area as being typical. "William H. Edwards, when he rearranged his collection before transmitting the same to me, restricted the specific name montis to a long series of specimens most of them bred from larvae obtained in Colorado." (Holland, 1931). These specimens are in fact assignable to either A. celtis antonia or A. celtis celtis, thus further complicating the identity of A. antonia.

Holland (1931) also stated, "Edwards.. labeled in his own handwriting as antonia, a specimen which bears the label 'Colorado, Dodge, type of antonia,' and which agrees thoroughly with other specimens labelled as antonia from Texas and Arizona." This specimen was the one mentioned in the original description of A. antonia variety montis (Edwards, 1883) and which in fact is labelled, "Antonia [male]/Colo. Dodge; type of v. montana." Apparently Holland did not resolve the identities of these butterflies according to accepted taxonomic rules and procedures, preferring to rely on Edwards' relabelled specimens. Barnes and McDunnough (1913) were the first to unravel this taxonomic confusion. The problem was finally settled by Brown in 1967 by lectotype designations.

Populations at the edges of the range of this species are the most extreme phenotypically. One such population, called here "mexicana," occurs in southern Texas into northeastern Mexico where it is sympatric with *A. clyton louisa*. It has not yet been possible to define this population geographically in Texas and it seems to blend (clinally) into central Texan *A. celtis antonia*.

Parasites reported to attack A. celtis include the hymenopterous parasites Telenomus sp. (Scelionidae) of eggs and Elachertus sp. (Eulophidae) of last instar larvae, and the fly, Euphorocera prob. floridensis Townsend (Tachinidae), in larvae of A. celtis celtis (Friedlander, 1984). A few eggs of A. celtis antonia were found to be parasitized with trichogrammatids in central Texas.

The predator *Polistes exclamans* Viereck (Hymenoptera, Vespidae) of fifth instar larvae attacks individuals of *A. celtis antonia* (Friedlander, 1984).

# Asterocampa leilia (W. H. Edwards, 1874)

(Genitalia, Figure 5)

Synonymy and discussion of types

Apatura leilia W. H. Edwards, 1874; F. M. Brown, 1967 (designation of lectotype)

Apatura leila, H. Skinner, 1891 (misspelling)

Apatura celtis? variety leilia, H. Strecker, 1878

Apatura cocles, W. H. Edwards, 1884 (manuscript name); J. A. Lintner, (1885) (original description)

Apatura celtis, E. M. Aaron and S. F. Aaron, (1885) (part))

Apatura alicia variety leilia, J. B. Smith, (1884)

Apatura alicia, J. B. Smith, (1884) (misidentification)

Doxocopa leilia, F.D. Godman and O. Salvin, (1884)

Doxocopa celtis, F. D. Godman, (1901) (part)

Chlorippe leilia, W. J. Holland, 1898 Chlorippe cocles, H. G. Dyar, [1903]

Chlorippe celtis variety antonia, H. Skinner, 1911 (part)

Chlorippe celtis variety leilia, H. Skinner, 1911

Asterocampa leilia, J. Röber, 1916; W. J. Holland, 1931; J. McDunnough, 1938; H. Stichel, 1938; C. C. Hoffmann, 1940; A. B. Klots, 1951; J. A. Comstock, 1953 (biology); K. Maeki and C. L. Remington, 1960 (karyotype); C. F. dos Passos, 1964; L. D. Miller and H. K. Clench, 1968 (biology); J. A. Scott, 1973 (biology), 1975 (biology); W. H. Howe, 1975; G. T. Austin, 1977 (biology); R. M. Pyle, 1981; L. D. Miller and F. M. Brown, 1983

Asterocampa leila, J. A. Comstock, 1961; P. R. Ehrlich and A. H. Ehrlich, 1961; L. D. Miller and F. M. Brown, 1981 (misspellings)

Asterocampa leilia form cocles, H. Stichel, 1938; D. B. Stallings and J. R. Turner, 1947; A. B. Klots, 1951

Asterocampa leilia cocles, C. F. dos Passos, 1964; L. D. Miller and F. M. Brown, 1983

Asterocampa leila cocles, L. D. Miller and F. M. Brown, 1981 (misspelling)

Asterocampa cocles, J. McDunnough, 1938; C. F. dos Passos, 1964

Asterocampa celtis race antonia, J. S. Garth, 1944 (misidentification)

Asterocampa montis, R. M. Pyle, 1981 (misidentification, part: p. [284])

Celtiphaga leilia, W. Barnes and F. H. Benjamin, 1926

Celtiphaga cocles, W. Barnes and F. H. Benjamin, 1926

This species was originally described from 2 males taken in August 1874 by a member of the Wheeler Expedition "at Camp Lowell and in Sonoto [sic] Valley, Arizona" (Mead, 1876). Brown (1967) selected a lectotype which together with the paratype is deposited in the Carnegie Museum of Natural History. Both have been examined.

Lintner's *Apatura cocles* was described from 2 females which he collected in the spring of 1877 in Hidalgo, Texas. He published the manuscript (written in 1880) in 1885 after it had been circulated in the East. These female specimens from Texas in the spring exhibited a phenotype quite different for the species than the type specimens of *A. leilia*. The latter are males from Arizona collected in the late summer. Even so, *A. cocles* was recognized as being the same as *A. leilia* shortly after it was described (Aaron and Aaron, 1884 (1885). Edwards was unfamiliar with the specimens at the time he saw Lintner's manuscript and included *A. cocles* as a Lintner manuscript name in his list (1884a) although he had probably seen females of *A. leilia* by that time from Arizona (from Doll: Edwards, 1883).

One of the 2 syntypes is in the New York State Museum, Albany and the other in the Carnegie Museum of Natural History. The latter syntype is here designated as the lectotype. It is labelled, "Apatura, cocles. [Female], Lintn., 5861. TYPE," "Linnert [sic], Rio Grande," "Sm. No. 189, det. Skinner," "collect., Skinner," "Asterocampa, leilia (Edw.) [female], det. W. J. Reinthal," "Exch. A. N. S. P., C. M. Acc. 20359.," "Holotype, Apatura, cocles Lintner," "Insect collection, Carnegie Museum of, Natural History, Pittsburgh, Pa. (CMNH)."

# Diagnosis

A. leilia belongs to the Celtis group of Skinner (1911). This species is unique in that it uses only one species of hackberry, Celtis pallida Torr., as a larval host and is not likely to be found on any other. There are chemical and morphological differences between species of this subgenus of hackberry (Momisia) and that of the tree species. A. leilia overlaps the range of A. celtis antonia in Texas, Mexico and Arizona, the only member of the Celtis group with which it is sympatric and is often confused. Only the "mexicana" population of A. celtis antonia is known to use C. pallida as a larval host plant.

Eggs of *A. leilia* differ from those of other members of the Celtis group by having a thicker chorion and smaller aeropyles.

Larvae of *A. leilia* differ from members of the Celtis group by having more strongly developed dentition and branched head setae in the first instar. The antlers of mature larvae are proportionately longer while other head scoli are shorter. The whole head capsule is thicker and less hairy. The body setae are shorter and cuticle thicker. Dentition is more pronounced in mature larvae as well.

Larvae of A. leilia are solid green with dorsolateral and subspiracular

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yellow longitudinal stripes, whereas *A. celtis antonia* larvae routinely have some lateral yellow crenations or diagonal stripes. *A. leilia* larvae have green faces centrally but are variously brown dorsally and laterally elsewhere on the head. The antlers resemble the spination of the host plant. *A. celtis antonia* larvae have brown antlers and from green to brown heads. Intermediate forms of *A. celtis antonia* have brown streaks from the mandibles up the the antlers, on a green background.

A. leilia pupae are unique among hackberry butterflies by having a reduced cremaster, the hooks spanning only half the distance from the posterior tip to the sustainers. As a consequence, the pupae hang away from their substrate (usually a twig instead of a leaf) instead of being flush against it. The effect is that of being very leaf-like instead of being hidden by a leaf. Pupae are surprisingly hairy, with the setae being bent at right angles as possibly an adaptation for moisture retention. There is very little in the way of light markings on carinae such as are found on pupae of A. celtis antonia except for those on the wing edges and the dorsal crest.

Adult butterflies have the wing shape of members of the Clyton group but the color pattern of the Celtis group. As Edwards (1874) stated, "[Leilia is] allied to Celtis, but with the shape of Clyton." Both discal bars are unbroken, most eye-spots are well developed, and the FW postmedian spots are distinctly white. Other Celtis group taxa have a broken discal bar, often have a few eye-spots reduced, and the FW postmedian spots tend to be yellowish.

# Descriptions of life stages

The mature larva and pupa were described by J.A. Comstock (1953). The larva was illustrated on the wrong host plant, *Celtis reticulata*, instead of *Celtis pallida*. The latter is the correct host. The figured pupa was attained through rearing and was slightly misshapen.

## EGGS AND EGG DEPOSITION:

Egg with 19 or 20 ribs, 0.9 mm wide, sculpturing obscured by thickened chorion, micropylar area in 3 ranks, 9 petals in rosette, aeropyles very small. Eggs deposited in small clusters (3-15) on either side of leaves of host plant. Egg yellowish white.

## LARVAE:

First instar larva with brownish black head capsule and green body, 2.6 mm long. Head capsule 0.6 mm wide, excluding scoli, setae barbed; 5 pairs of scoli prominent, twice width of simple eye. Mandiables 4-toothed. Body setae as long as those on head, also barbed. Prolegs with well developed crampets. Anal area short spinose; anal horns long, light brown.

Second instar larva with well developed antlers and long lateral head scoli, body length 3.9 mm. Head capsule 0.85 mm wide, excluding scoli. Dark brown head, green body, with some indication of dorsolateral longitudinal stripes.

Third instar larva 0.8 mm long, with noticeably short body setae and heavily sclerotized head capsule. Certain sets of body chalazae have fused bases.

Diapausing form with smaller head and shorter, clubbed antlers. Head capsules 1.1-1.3 mm wide. Brown head, green body, with beginnings of subdorsal and supraspiracular, yellow longitudinal stripes.

Fourth instar larval head capsule takes on typical *A. leilia* look with squarish head and long, short-branched antlers, width 1.8-2.2 mm. Coloration as in fifth instar.

Fifth instar larval head capsule 2.5-2.8 mm wide; body with very short setae dorsally. Texas populations generally with longer head scoli than those of Arizona. Mandibles still with teeth, the one incisor with a wavy edge. Antlers 1.7 mm long, AL about as long as antler is wide, longer than AM. AT1 and AB1 short, AB2 long, AB3 short, AB4 very short, AB5 short. V1 and V3 short, V2 vestigial. L1 long, 0.7-0.9 mm. O2 same length as AB2, O3 slightly shorter. Other head scoli short or vestigial as shown. Antlers dark reddish brown to black, concolorous with top and sides of head capsule; face green except for stemmatal region, upper part of median facial sclerite, which are also dark brown. Labrum and sides of face (where green meets brown) light colored (yellowish white). Body olive green, nonreflective, almost grayish green, matching the coloration of host plant leaves, heart-line barely showing. Dorsolateral and subspiracular longitudinal stripes yellowish white, more intense on thorax, running from head capsule to short anal horns. Spiracles whitish to light green. Texan larvae with lighter head capsules, reddish brown less extensive, head often green laterally. Total length about 27 mm.

## PUPAE:

Pupa typical of *Asterocampa*, except for shortened cremastral bed of hooks, 1.45 mm. Pupa about 15-18 mm long, 4.5 mm wide, 6.8-8.5 mm high. Head with short prolongations; eyes each with small tubercle. Abdominal crest not abrupt, divisions between segments noticeable but not serrated, anterior segmental portions blunt (not spinose). Crest, head carinae and edges of wings marked with light yellow; rest of body olive green, blending into coloration of leaves. Texas pupae with more light-colored markings especially laterally on abdominal segments in the form of speckles, a subspiracular line, and the beginnings of diagonal stripes. Reduced cremaster holds pupa away from substrate at about 30 degree angle.

#### ADULTS:

Asterocampa leilia (Pl.21, figs. A-C) antennal scape and pedicel white-scaled; flagellar segments (36-44) scaled dorsally with dark brown ending distally with white scales, bare ventrally between carinae. Club virtually bare, composed of 12 segments, cuticle dark brown dorsally and laterally on first 5, pale yellow orange beyond. Frons black, scaled on dorsal two-thirds with short whitish scales intermixed with long, light grayish brown hair-scales. Palps with short white and long pale yellow scales on basal 2 segments. Basal segment with brush. Second and third segments with brown scaling laterally and medioventrally. Third segment mainly brown, except for white tip and ventral long-scales. Occiput with short white strap- and long light grayish brown hair-scales. Body dorsally orange rufous short-scaled, with grayish brown hair-scales, black cuticle of thorax showing through. Abdomen appearing more orange. Body ventrally mainly white with scattered brown. Forelegs white. Middle and hindlegs dorsally pale yellow orange.

Costal FW length (fig. 4) 20-25 mm (male,  $22.1\pm1.4$  mm, n=54), 23-30 mm

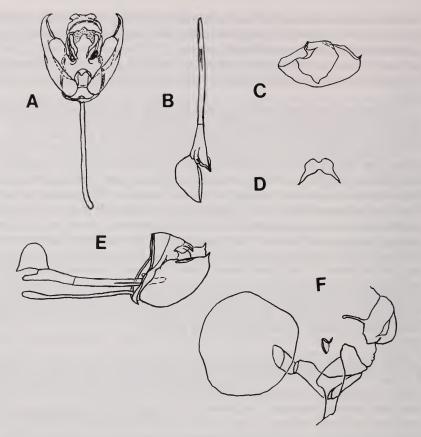


Fig. 5. Genitalia of Asterocampa leilia (Edwards). Male genitalia:

Whole genitalia (**A**, ventral view, valves spread) with aedeagus (**B**) separate: Texas: Dimmit Co., Chaparral Wildlife Management Area, July 1977, A. Lewis, coll. TF gen. prep. 1977.

Right valve (**C**, mesal view) and uncus (**D**, ventral view): Mexico: Veracruz, Jalapa, no date, CMNH. TF gen. prep. no. 1982-9.

Whole genitalia (**E**, left lateral view): Arizona: Pima Co., Soldier Canyon, April 1928, CMNH. TF gen. prep. no. 1982-99. *Female genitalia*:

Whole genitalia (**F**, left lateral view): Arizona: Pinal Co., 10 mi. w. Superior, May 1978, CMNH. TF gen. prep. 1982-47.

(female,  $26.1\pm1.6$  mm, n=24); females from Texas generally larger than those of Arizona and central Mexico.

Male genitalia (Fig. 5A-E) with moderate saccus (2.1-2.4 mm) and aedeagus (2.9-3.0 mm). Valves 1.5-1.7 mm long with developed costal ridge and short terminal spine. Uncus reduced, lobes flattened posterolaterally, notch slight. Anal tuft present, hair-scales straight. Female genitalia, (fig. 5F) with short, sclerotized ductus (0.7-1.5 mm) meeting long ostiolar funnel. Corpus bursae with a pair of signa, in longitudinal strips on the right side, sometimes not well sclerotized. Anal papillae not emarginate.

Photographs of adults published in: Brown, 1967 (Fig. 20, lectotype, male, d, v); Ferris and Brown, 1981 (p. 356, male, d); Pyle, 1981 (Plate 662L, male, v; Plate 663L, male, d); Pyle, 1985 (Plate 662L, male, v; Plate 662R, male, d); Scott, 1986 (Plate 19 [figs.] 141a, male, d; 141b, male, v); Wright, 1906 (Plate XXIII: fig. 246, male, d). Howe (1975) excellently figured individual specimens (Plate 11: fig. 13, female, d; fig. 15, male, d; fig. 15, female, v).

Forewings dorsally with basal ground color strong orange (a rich, intense orange) infuscated with grayish brown at base; dark brown distally, changing in reflectance to more reddish when viewed at an angle; costal margin orangish out towards apex. Two discal bars dark brown with reddish brown centers, pale orange-yellow between. Postmedian spots in zigzag pattern (R5-A2), white anteriorly, pale yellow posteriorly; spots bordered basally with dark brown. Limbal spots white in R5 and M2, brownish black with whitish pupils in M1 and M3, brownish black in Cu1. Spots M3 and Cu1 ringed with strong orange. Ocellus Cu2 represented by strong orange spot, sometimes with black center. Veins dark brown, as are submarginal and marginal bands. Fringe dark brown with white centrally in triads in cells R5 to Cu2+A1.

Dorsal HW ground color strong orange, except anal cup and costal cell, which are light gray. Discal cell faintly 2-barred, reddish brown with mixed dark brown scaling. Postmedian spots pale yellow, bordered basally with reddish brown with mixed dark brown, obscure. Limbal spots brownish black in local fields of orange-yellow, with at least spot Cu1 pupilled with bluish white. Veins dark brown. Submarginal band crenated dark brown; marginal band dark brown; fringe checkered as in FW cells Sc+R1 to Cu2+A1. Hair-scales cover lower basal portion of wing to hind angle, pale orange.

Forewings ventrally dark grayish brown above Cu2 and chestnut brown basally in cell Cu2+A1. Discal cell 2-barred, dark brown with lighter middles, white between. Postmedian spots whitish, the more posterior ones tinged with brown, bordered basally with dark brown. Limbal spots as follows: R5 white; M1, M3 Cu1 dark brown with whitish blue pupils in strong yellow ring; M2 dark brown with yellow ring basally, white distally. Submarginal band brown, broken into crescents; marginal band dark brown, appearing almost purplish, in field of grayish scaling such as dusts anterior margin of FW and basal half of HW. Veins brown.

Hindwings ventrally largely cast in grayish scaling except margins of spots and other features of wings. Bars of discal cell dark brown in outline; similar spot basally in cells Sc+R1 and Rs. Postmedian spots whitish, bordered basally with dark brown. Limbal spots dark brown with whitish blue pupils in strong yellow rings bordered by dark brown, Sc+R1 to A2; Cu2 and A1 spots joined at yellow ring.

Variation observed among individuals included larger whitish blue pupils on limbal spots, decreased size of limbal and postmedian spots, darker scaling between discal bars dorsally, broader fields of orange surrounding limbal HW spots dorsally (females), dorsal ground color almost yellow-orange (spring season specimens, especially from Arizona)

## Range

A. leilia (Plate 2): Southern Texas and Arizona, northern Mexico: Gila River drainage in southern one-half of Arizona, south into Sonora

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and Baja; Rio Grande drainage, except Pecos River, northward to Llano Basin in Texas; in northeastern Mexico, rivers in the Chihuahuan desert, and river drainages from Nuevo Leon to Veracruz. Specimens examined (states listed alphabetically, by county; over 850 non-reared adults):

MEXICO: Chihuahua, Coahuila, Durango, Nuevo Leon, Sonora, Tamaulipas, Veracruz [states]

U.S.A.: ARIZONA: Cochise, Gila, Maricopa, Pima, Pinal, Santa Cruz. Yavapai; NEW MEXICO: Hidalgo; TEXAS: Bexar, Brewster, Cameron, Frio, Hidalgo, Jeff Davis, Kerr, Live Oak, Maverick, Presidio, Starr, Terrell, Uvalde, Val Verde, Webb, Zapata; UTAH: Weber [extremely dubious record].

The distribution of this butterfly is coincident with that of its host plant, Celtis pallida Torrey. It occurs at lower altitudes, in arroyos, canvons, chaparral and thorn forest. The Weber Co., Utah record is outside the known distribution of its host (Benson and Darrow, 1945) and must be considered either a misidentification or a mislabeling. The Washington Co., Utah record of Callaghan and Tidwell (1971(1973)) is probably A. celtis antonia ["montis"] (Gillette, pers. comm.). The specimens reported as A. leilia from the Grand Canyon (Garth, 1950) are actually A. celtis antonia ("montis") (Reinthal, unpublished obs.). A. leilia has recently been documented to occur in Baja California del Sur, Mexico (Brown and Faulkner, 1984).

#### Discussion

Asterocampa leilia is unique among hackberry butterflies in that it utilizes only spiny hackberries (Celtis subgenus Momisia) as larval food plants. Larvae and adults (Austin, 1977; pers. obs.) are active at high temperatures. Males prefer perches on the ground. Adults are commonly sap-feeders but are also found at flowers, scat and rotting fruit. They are often found in association with A. celtis antonia.

Adults of *A. leilia* are often and easily confused with *A. celtis antonia*. A. leilia was discovered at the same time as the western populations of A. celtis were being described and because it was not very different in pattern or hue was often included as another western form of A. celtis.

The distinctness of this species is best seen by its host plant utilization and in its larvae and pupae which are adapted to the host plant and high temperatures. Larvae and pupae are virtually impossible to locate on Celtis pallida because they are cryptically colored and of a similar size to the leaves. Larval antlers resemble developing paired spines of the plant. Pupae hang at an angle resembling a leaf.

Egg parasites (hymenoptera: Scelionidae, Telenomus sp.) have been reported for this species (Friedlander, 1984).

Asterocampa clyton (J. B. A. Boisduval and J. E. Le Conte, [1835]) (Genitalia, Figure 6)

Synonymies and discussion of types

Asterocampa clyton clyton (J. B. A. Boisduval and J. E. Le Conte, [1835])

Apatura clyton J. B. A. Boisduval and J. E. Le Conte, [1835] (biology); W. H. Edwards, 1877 (biology), 1881 (biology), 1884 (biology), 1884 (evolution); M. E. Murtfeldt, (1886) (biology); H. Edwards, 1889 (biology); L. O. Howard, 1894 (ecology)

Apatura elyton, W. A. Pearce, 1894 (misspelling)

Apatura proserpina S. H. Scudder, (1868); F. M. Brown, 1983 (citation)

Apatura idyja, W. F. Kirby, 1871 (part)

Apatura idyja, W. V. Andrews, 1875 (misspelling, part)

Apatura herse, C. V. Riley, 1873 (biology), 1874 (biology)

Apatura hyrse, H. G. Knaggs et al., (1874) (misspelling)

Apatura clyton variety proserpina, W. H. Edwards, (1876) (biology); C. J. Maynard, 1891

Apatura clyton dimorphic variety proserpina, W. H. Edwards, 1877, 1884; W. Osburn, 1895 (excluded name)

Apatura clyton aberration proserpina, H. Strecker, 1878

Apatura clyton variety ocellata W. H. Edwards, (1876); J. B. Smith, 1903

Apatura proserpina S. H. Scudder, (1868)

Apatura proserpina ocellata, W. G. Wright, 1905

Apatura clyton aberration male nig. H. Strecker, 1878 (abbreviated name, excluded name)

Apatura clyton nig J. B. Smith, 1903 (misspelling, change in status)

Doxocopa herse, S. H. Scudder, 1871 (1872)

Doxocopa clyton, F. D. Godman and O. Salvin, (1884)

Chlorippe herse form clyton, S. H. Scudder, 1875

Chlorippe herse, S. H. Scudder, 1881

Chlorippe clyton, S. H. Scudder, 1888 (biology, morphology), 1889 (biology);
W. J. Holland, 1898 (biology);
J. W. Tutt, (1906) (biology);
R. A. Leussler, 1913 (evolution);
V. Randolph, 1929 (evoluation);
A. H. Clark, 1932 (biology)

Chlorippus clyton, W. T. Davis, 1924 (misspelling)

Chlorippe herse variety proserpina, S. H. Scudder, 1875, 1889; H. Engel, 1908;R. A. Leussler, 1913 (evolution); F. E. Watson, 1920 (evolution)

Chlorippe clyton variety nig, H. Skinner, 1911

Asterocampa lycaon, J. Röber, 1916 (part)

Asterocampa lycaon aberration ocellata, J. Röber, 1916 (excluded name)

Asterocampa clyton, W. J. Holland, 1931 (biology); J. McDunnough, 1938; H. Stichel, 1938; R. W. Macy and H. H. Shepard, 1941 (biology); G. Ehle, 1950 (biology); A. B. Klots, 1951; C. F. dos Passos, 1964; R. Heitzman, 1965 (biology); P. R. Ehrlich and A. H. Ehrlich, 1961 (part); W. H. Howe, 1975; J. A. Scott, (1981) (biology); R. M. Pyle, 1981) L. D. Miller and F. M. Brown, 1981, 1983; P. A. Opler and G. O. Krizek, 1984 (biology)

Asterocampa clyton aberration nig, J. McDunnough, 1938 (excluded name) Asterocampa clyton from nigra, H. Stichel, 1938

Asterocampa clyton form proserpina, J. McDunnough, 1938; H. Stichel, 1938 Asterocampa clyton form ocellata, H. Stichel, 1938

Asterocampa clyton form "apunctus" J. A. Scott, 1981 (excluded name)

Celtiphaga clyton, W. Barnes and F. H. Benjamin, 1926

Celtiphaga clyton aberration nig, W. Barnes and F. H. Benjamin, 1926 (excluded name)

Celtiphaga clyton form proserpina, W. Barnes and F. H. Benjamin, 1926

Like A. celtis, A clyton is based on a drawing by John Abbot of Georgia. Any specimens used for the drawing are presumed destroyed so that the figure itself must be considered as the type. The lectotype (Brown, 1967) of A. clyton var. ocellata Edwards (female, Coalburgh, West Virginia) is in the Carnegie Museum of Natural History and has been examined. The type of Scudder's A. proserpina (female, Iowa) has not yet been located. It was not found at the Museum of Comparative Zoology at Harvard University where it was last reported to be deposited (Miller and Brown, 1981). Both names have been long known to represent color forms. The male type (Berks Co., Pa.) of Apatura clyton nig J. B. Smith, 1903, is in the Strecker Collection presently housed at the Allyn Museum of Entomology in Sarasota, Florida. Poorly marked "apunctus"-like individuals (Scott, 1981) occur in virtually all populations of A. clyton.

# Asterocampa clyton flora (W. H. Edwards, 1976)

Apatura clyton variety flora W. H. Edwards, (1876); H. Edwards, 1889 (biology) Apatura flora, W. H. Edwards, 1881 (biology), 1882 (biology), 1884 (biology), (1891) (biology)

Chlorippe flora, W. J. Holland, 1898

Chlorippe clyton variety flora, H. Skinner, 1911

Asterocampa lycaon form flora, J. Röber, 1916

Asterocampa flora, W. J. Holland, 1931; W. H. Howe, 1975; L. D. Miller and F. M. Brown, 1981, 1983; R. M. Pyle, 1981

Asterocampa clyton, P. R. Ehrlich and A. H. Ehrlich, 1961 (part)

Asterocampa clyton flora, J. McDunnough, 1938; H. Stichel, 1938; L. Harris, Jr., 1950 (biology); A. B. Klots, 1951; W. M. Davidson, 1958 (biology); C. F. dos Passos, 1964; P. A. Opler and G. O. Krizek, 1984

Celtiphaga clyton flora, W. Barnes and F. H. Benjamin, 1926

This taxon is based originally on several males and a female collected in Palatka, Florida. Brown (1967) designated (with Reinthal) one of the males as lectotype which together with the remaining type series is housed in the Carnegie Museum of Natural History. These have been examined.

# Asterocampa clyton texana (H. Skinner, 1911)

Apatura flora, E. M. Aaron and S. F. Aaron, (1885); F. H. Snow, (1906) (misidentifications)

Chlorippe clyton variety texana H. Skinner, 1911; W. Barnes and J. Mc-Dunnough, 1913

Chlorippe flora, J. K. Strecker, 1925 (misidentification)

Chlorippe clyton subpallida W. Barnes and J. H. McDunnough, 1913 (new synonym)

Asterocampa lycaon, J. Röber, 1916 (part)

Asterocampa texana, W. J. Holland, 1931; J. A. Comstock, 1961 (biology); W. J. Reinthal, 1966 (biology); W. H. Howe, 1975; L. D. Miller and F. M. Brown, 1981, 1983; R. M. Pyle, 1981

Asterocampa subpallida, W. J. Holland, 1931; J. A. Comstock, 1953 (biology); C. F. dos Passos, 1964; W. H. Howe, 1975; L. D. Miller and F. M. Brown, 1981, 1983; R. M. Pyle, 1981

Asterocampa clyton texana, J. McDunnough, 1938; H. Stichel, 1938; A. B. Klots, 1951; C. F. dos Passos, 1964; R. W. Neck, 1977 (biology); C. J. Durden, 1982 (evolution)

Asterocampa clyton subpallida, J. McDunnough, 1938; H. Stichel, 1938; W. D. Field, 1940 (partial misidentification); J. A. Scott, (1981) (biology)

Asterocampa leilia, J. A. Comstock, 1953 (misidentification, part: pp. 130-132) Asterocampa clyton, P. R. Ehrlich and A. H. Ehrlich, 1961 (part)

The male holotype, female allotype and other specimens of the type series of *Chlorippe clyton* from *texana* (Round Mountain, Texas) are in the Carnegie Museum of Natural History. Syntypes (2 males, 4 females) of *Chlorippe clyton subpallida* (Baboquivera [sic] Mts., Pima Co., Arizona) are in the National Museum of Natural History, Smithsonian Institution. The male lectotype is designated here ("Babaquivera [sic], Mts. Ariz., Pima Co." "C. clyton, v. subpallida, Type [male] B & McD" "Photograph, Pl. 2 No. 7" "Aug") and is housed in the museum type collection.

Asterocampa clyton louisa (D. B. Stallings and J. R. Turner, 1947)

Asterocampa clyton louisa D. B. Stallings and J. R. Turner, 1947; A. B. Klots, 1951; C. F. dos Passos, 1964

Asterocampa louisa, W. H. Howe, 1975; L. D. Miller and F. M. Brown, 1981, 1983; R. M. Pyle, 1981

The holotype male of *Asterocampa clyton louisa* (Pharr, Texas) is in the Yale Peabody Museum. It has not yet been examined.

# Diagnoses of taxa

Asterocampa clyton belongs in the Clyton group of hackberry butter-flies. The nominate subspecies differs from A. clyton texana and the similar A. clyton lousia in both larval and adult stages. The caterpillars are routinely fully striped whereas those of A. clyton texana and A. clyton louisa generally lack subdorsal and lateral banding, being marked only with crenations and lines. Adults are tawny, contrastingly marked with dark brown, and exhibit dark morphs in which the

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hindwing limbal spots are partially ("ocellata") or fully obscured ("proserpina"). Spot Cu1 of the FW is not ringed. Cu1 ringed is the condition commonly seen in *A. clyton texana* and *A. clyton louisa*.

A. clyton flora differs only slightly from the nominate subspecies. Larvae routinely have shorter antlers than their more northern and western counterparts; adults are considerably larger and more colorful, the browns of the wing apices being replaced by a brick red orange; dark forms "proserpina" and "ocellata" are virtually absent in both sexes. It differs from A. clyton texana and A. clyton louisa by the same characters as does A. clyton clyton. A. clyton flora occurs in peninsular Florida and forms hybrid zones with typical A. clyton clyton on both the Gulf and Atlantic coasts. There is a tendency of both large size and bright coloration in populations of A. clyton clyton along the Gulf Coast producing an adult phenotype similar to A. clyton flora.

The larvae of *A. clyton texana* and *A. clyton louisa* have longer antlers than found in the other subspecies and the body color is mostly green (with lines and crenations of yellowish white) rather than being typically striped. Larvae of *A. clyton texana* generally have heads which are mostly green whereas those of *A. clyton louisa* are typically mostly dark brown. Adults of both subspecies are far less orange than the adults of the eastern subspecies and tend to have lighter ground colors of tan. The apices of the forewings of *A. clyton louisa* are very dark. Limbal spot Cu1 of the FW is often ringed with darker scaling. Limbal spots of the HW below are often "washed out," especially in *A. clyton texana* form "subpallida." Dark forms in either sex have not been reported but a few such individuals occur in both wild and laboratory populations. *A. clyton texana* and *A. clyton louisa* will be discussed together in the following descriptions

# **Descriptions of life stages**

Immature stages of *A. clyton clyton* were described in detail by Riley (1874), Edwards (1876, 1884d), and Scudder (1889). Immature stages of *A. clyton flora* were described by Edwards in 1881 and 1891. Stamp (1983) reported on the diapause behavior of third instar larvae. Immature stages of *A. clyton texana*, forms "subpallida" (first instar, second instar, mature larva and pupa) and "texana" (all immature stages), were described by J.A. Comstock in 1953 and 1961, respectively. Scott (1986; Pl.2 [fig.] 142; Pl.4 [fig.] 142) photographically illustrated the mature larvae and pupa of *A. clyton clyton*.

## EGGS AND EGG DEPOSITION:

Egg of *A. clyton clyton* 19-22 ribbed, 0.7-0.9 mm wide by 0.7-0.9 mm high. Micropylar rosette with 11 petals. Sculpturing smooth, cross-ribbing and aeropyles only apparent on upper half of eggs. Eggs of *A. clyton flora* light yellow, also in large masses, tightly packed in many layers, usually deposited on the undersides of leaves of the larval host plant *Celtis laevigata* Willd. Edwards

(1881, 1891) reported eggs of *A. clyton flora* yellow-green, with 16-20 vertical ribs and 3-4 concentric rows of polygonal areoles in micropylar rosette.

Eggs of *A. clyton texana* and *A. clyton louisa* with thick sculpturing, usually with 20 ribs (18-21), micropylar rosette with 8-12 petals, more western populations (*A. clyton texana* form "subpallida") tending to have fewer petals. Aeropyles only on upper halves of longitudinal ribs. Eggs 0.7-1.0 mm wide, 0.9-1.0 mm high, deposited in moderately large, tightly packed clusters.

## LARVAE:

First instar larval head capsule of *A. clyton clyton* tan to dark brown, usually light brown, 0.6 mm wide, with poorly developed head scoli about size of simple eye. Setae of head capsule and body extremely short-branched. Total body length 3.7 mm. Prolegs with crampets; setae unbranched. Body color light green. Anal horns very short. First instar larval head capsule of *A. clyton flora* tan; body light and dark green striped. Total length about 4 mm. First instar larval head capsule of *A. clyton texana* and *A. clyton louisa* light to medium brown, 0.6 mm wide, poorly developed, head scoli short, about size of stemmatal width. Setae of head capsule extremely short-branched (barbed). Body yellowish green; anal horns short. Total length about 4 mm.

Second instar larva of *A. clyton clyton* with patterned brown and cream-colored brown head capsule. Antler base greater than mandibular width. AB5 about 3/4 length of L1. Scoli V2 present. Body green, striping apparent in this stage, consisting of 3 yellow stripes on each side of a darker green heart-line. Anal horns light green. Total length about 4 mm. Second instar larva of *A. clyton flora* with variegated head capsule, half brown. Antlers wider at base than mandibles are wide. AB5 about 3/4 length of L1. V2 present. Body striped as in mature larva. Anal horns unpigmented. Total length between 3 and 4 mm. Second instar larval head capsule of *A. clyton texana* variably marked with brown. Capsule 0.9 mm wide, with conical scoli, antler base wider than mandible, AB5 about 3/4 of L1 in length. Head narrower at level of antlers than at mandibles, not square. Body striped with green and yellowish green. Anal horns unpigmented to light tan. Total length about 6 mm. Second instar larva of *A. clyton louisa* similar to that of *A. clyton texana*, but generally with darker brown head capsule.

Third instar larva of *A. clyton clyton* with mottled brown head capsule. Diapausing larva with reduced antlers. Total length about 7.5 mm. Third instar larva of *A. clyton flora* also with variegated head capsule. Body marked as before. Diapausing larva with reduced antlers. Total length 5 to 6 mm. Third instar larval head capsule of *A. clyton texana* variable, but mostly brown with long scoli (non-diapausing), 1.2-1.5 mm wide. Body striped as in second instar. Total length about 6 mm. Third instar larva of *A. clyton louisa* similar, but yellows more intense, head capsule mostly dark brown.

Fourth instar larva of *A. clyton clyton* with variegated brown head capsule. Total length up to about 20 mm. Fourth instar larva of *A. clyton flora* with brown-streaked head capsule, antlers rather short. Green morphs occasionally occur, with only front of antler brown. Body striped as in mature larva; total length over 10 mm. Fourth instar larval head capsule of *A. clyton texana* variably brown, with long scoli, AL and AM of antler rounded and thick. Head capsule width 2.4-2.5 mm wide. *A. clyton louisa* with darker head capsules with longer antlers. Total length about 13 mm; pigmented as in mature larva.

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Fifth instar larva of  $A.\ clyton\ clyton$  green with (usually) green head capsule which has 4 vertical, white stripes (unpigmented areas); antlers have brown dot anteriorly. Heart-line dark green. Subdorsal bands yellow and white, the inner one light yellow with intermittent yellowish white folds, separated from outer by intermittent green. Dorsolateral portion yellowish white. Subdorsolateral area green with lighter center; yellowish white chalazae punctuate center. Supraspiracular band yellowish white. Spiracular area green with yellowish green center; chalazae apparent. Subspiracular stripe yellowish white. Prolegs, venter, and thoracic legs light to medium green. Anal horns long. Some individuals with considerably less yellow to banding. Total length 32-42 mm. Fifth instar larva of  $A.\ clyton\ flora$  green with yellow stripes, with dark brown and green head capsule striped with white; antlers rather short. Heart-line dark green. Subdorsal bands bright yellow, the inner portion more yellow than the outer, which is whitish and separated by a green line. Supra-and subspiracular bands yellow. Length of males, 30-38 mm, females, 35-44 mm.

Fifth instar larval head capsule of A. clyton texana with 1.4 mm long antlers, terminal pair of scoli rounded, broad. Head capsule around 3 mm wide. AT1, AB4 short, AB1 and AB3 slightly longer, AB2 longer still, with AB5 very long. V3, V1 and O3 moderately long, O2 longer (about same size as AB5), L1 longest of all (1.1 mm). AB5 to L1 ratio 0.80. Mandible with single incisor. Larvae light green with variably colored head capsules. Capsules are more often green with 4 whitish vertical streaks and a brown spots anteriorly on the antler in the more arid areas of the range (e.g., "subpallida"). A. clyton louisa larvae with dark brown head capsules. Heart-line a darker green line than general body color, sometimes invaded by spots of light yellow from the inner portion of the subdorsal bands. Subdorsal bands represented most often only by yellowish white dorsolateral line. Dorsolateral line sometimes intermittent, line alternating with spots of light yellow found in inner subdorsal area, such as normally found in A. clyton louisa mature larvae. Supraspiracular area marked with diagonal yellowish white dashes or whitish crenated line. Subspiracular line yellowish white. Anal horns moderately long, A. clyton louisa larvae generally much more colorful than those of A. clyton texana, with much more yellow and contrastingly colored head capsules, such as found in A. idyja argus. Total length about 32-36 mm.

#### PUPAE:

Pupa of *A. clyton clyton* 18-28 mm long, 7-11 mm high, head prolongations moderately long, somewhat blunt. Body color green, the dorsal crest marked with yellowish white, as are the posterior borders of the wings. Abdominal crest long, finely serrate, each segment with anterior tooth subtended by pair of small black spots. Pupae with cremastral pad lengths of 2.4-3.4 mm. Pupa of *A. clyton flora* 18-26 mm long, about 7-8 mm wide, and 10-12 mm high at maximum height. Head prolongations moderately long, somewhat blunt. Body yellowish green speckled with tiny whitish dots. Dorsal crest marked with whitish, as are veins and posterior edges of wings. Both supra- and subspiracular markings present. Abdominal crest finely serrate, each segment produced anteriorly into a spine subtended by pair of small black spots. Cremastral lengths of pupa 2.8-3.2 mm. Pupa of *A. clyton texana* 17-22 mm long, about 8 mm wide and up to 10 mm high at abdominal segment 3. Head prolongations moderate, blunt. Body light green flecked with white and with whitish markings along dorsal crest (more yellowish posteriorly) and posterior margins of wings. Wing veins and

supraspiracular regions (in diagonal bars) also marked with white. Abdominal crest somewhat serrate, anterior ends of segments ending in spines subtended by pairs of small black spots. Pupal cremastral lengths 2.5-3.0 mm. Pupa of A.  $clyton\ louisa\ similar\ to\ that\ of\ A.\ <math>clyton\ texana$ .

For a much more complete description of adults of this species the reader should consult my dissertation. Adults of the 4 subspecies differ mainly in coloration rather than pattern or morphology. Major differences among the adults are given in the descriptions to follow.

#### ADULTS:

Asterocampa clyton clyton (Pl.21, figs. D-I) antennae medium to dark brown, minutely ringed with lighter brown on flagellar segments giving faintly dotted appearance; apical portions slightly swollen, dark brown with bare pale yellow (tan with aging of preserved specimens) tips. Palps, general body scaling and ground color of wings above, strong yellowish orange, infuscated with dark brown. Forewing costal length (Fig. 4) A. clyton clyton 21-27 mm (males, 24.6  $\pm$  1.4m, n = 72), 26-34 mm (females, 30.6  $\pm$  1.7 mm, n = 34). Male genitalia (Fig. 6A-E) saccus 3.8-4.8 mm, aedeagus 4.3-5.7 mm, valves 2.2-2.6 mm, uncus bifid with narrow notch, dorsal brush with straight hair-scales. Female genitalia (Fig. 6F): ductus 2.8-3.1 mm, signum usually absent, when present 2 longitudinal strips.

Adults of A. clyton clyton illustrated by photographs: Brown, 1967 (female, lectotype of "ocellata," d, v); Ebner, 1970 (p. 96, male, d, v); Ferris and Brown, 1981 (p. 357, male, d, v; female, d); Harris, 1972 (Plate 6: fig. 5, male, d; fig. 6, female, d); Holland, 1898, 1931 (Plate XXIII: fig. 5, male, d; fig. 6, female, d); Lewis, 1973 (p. 13: fig. 7, male, d; fig. 8, female, v); Pyle, 1981, 1985 (Plate 666L, male, v; Plate 666R, female, d); Scott, 1986 (Plate 19 [fig.] 142d, male, d); Watson and Whalley, 1975 (pl. 216p, male, d). Howe (1975) illustrated individual specimens (Plate 11: fig. 10, male, v; fig. 16, male, d; fig. 17, female, d).

A. clyton clyton limbal spots yellow-orange, large, somewhat indented distally by submarginal band. In light phase, ground color basally strong yellowish orange, distally dark brown; hindwing above lighter. In dark phase, varying degrees of infuscation with blackish scaling, obscuring spots, especially in the hindwings.

Asterocampa clyton flora (Pl.21, figs. J-L) antennae of medium brown; apical portions as in nominate subspecies. Palps, general body scaling and ground color of wings above, strong orange. Forewing costal length (Fig. 4) of A. clyton flora 23.0-29.0 mm (males,  $26.8 \pm 2.1$  mm, n=12), 30.5-37.0 mm (females,  $33.8 \pm 2.4$  mm, n=9). Male genitalia of A. clyton flora similar to A. clyton clyton: saccus 3.6 mm, aedeagus 5.2 mm, valves 3.7 mm, uncus narrowly notched, dorsal brush with straight hair-scales. Female genitalia: ductus 2.2-2.8 mm long, signum composed of a pair of longitudinally wrinkled areas.

Adults of *Asterocampa clyton flora* illustrated by photographs in: Brown, 1967 (Fig. 22, male, lectotype, d, v); Harris, 1972 (Plate 6: fig. 7, male, d; fig. 8, female, d); Holland, 1898, 1931 (Plate XXIII: fig. 1, male, d; fig. 2, female, d); Pyle, 1981, 1985 (Plate 665, male, v, d); Excellent figures in Howe (1975: Plate 11: fig. 8, male, v; fig.18, male, d; fig. 19, female, d).

A. clyton flora limbal spots yellow-orange, adjacent to dark brown submarginal band. Ground color basally strong (yellowish) orange, distally dark

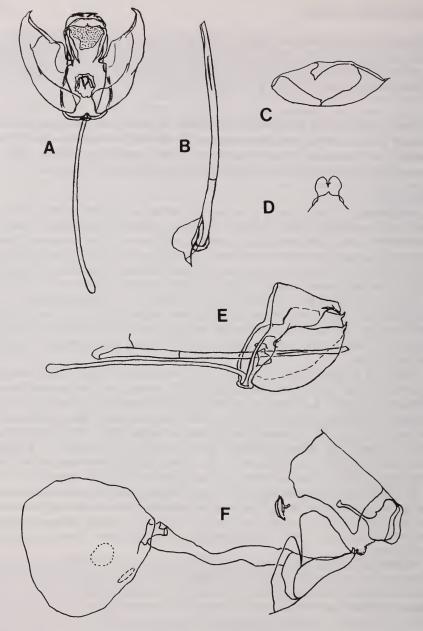


Fig. 6. Genitalia of Asterocampa clyton (B. & L.). Male genitalia:

Whole genitalia (**A**, ventral view, valves spread) with aedeagus (**B**) separate: Texas: Travis Co., Austin, September 1977, T. Friedlander. TF gen. prep. no. 1977. *A. clyton texana* (Skinner).

Right valve (**C**, mesal view) and uncus (**D**, ventral view): Nebraska: Douglas Co., Omaha, June 1913, CMNH. TF gen. prep. no. 1982-28. *A. clyton clyton*.

Whole genitalia (**E**, left lateral view): Texas: Travis Co., Austin, September 1977, T. Friedlander. TF gen. prep. no. 1977. *A. clyton texana*. *Female genitalia*:

Whole genitalia (**F**, left lateral view): Texas: Travis Co., Austin, September 1977, T. Friedlander. TF gen. prep. no. 1977. *A. clyton texana*.

brown (males) or brownish orange (tawny; females). Hindwing above paler, yellow-orange.

Asterocampa clyton texana (Pl.21, figs. M-O; Pl.22, figs. A-C) antennae of medium to dark brown, finely ringed with lighter brown on flagellar segments giving faintly dotted appearance when coloration constrasting; apical portions as before. Palps, general body scaling and ground color of wings above, light brownish orange. Asterocampa clyton louisa (Pl.19, fig. O; Pl.22, figs. D-F) antennae of very dark brown, only tips cream-colored. Palps, general body scaling and ground color of wings above, brownish orange, infuscated with dark brown. Forewing costal lengths (Fig. 4) of A. clyton texana: 23.0-29.0 mm (males, "subpallida",  $26.4 \pm 1.8 \text{ mm}$ , n = 50), 28.0-37.0 mm (famales, "subpallida",  $32.3 \pm 1.8 \, \text{mm}$ , n = 29);  $20.0 - 28.0 \, \text{mm}$  (males, "texana",  $24.3 \pm 1.5 \, \text{mm}$ , n = 118), 27.0-37.0 mm (females, "texana",  $31 \pm 2.3 \text{ mm}$ , n = 95); overall, 20.0-29.0 mm(males, n = 168), 24.5-37.0 mm (females, n = 124). Forewing lengths of A. clyton louisa: 22.0-26.0 mm (males,  $24.8 \pm 1.2 \text{ mm}$ , n = 17), 24.5-34.0 mm (females,  $30.3 \pm 2.7$  mm n = 9). Male genitalia of both subspecies as for A. clyton clyton: saccus 3.1-4.0 mm, aedeagus 4.1-6.9 mm, valves 2.1-2.3 mm, uncus narrowly notched, hair-scales of dorsal brush straight. Female genitalia of both subspecies: ductus 2.6-4.8 mm; usually without signum, but when present, 2 oval patches of polygonal reticulation on right side.

Photographs of adults of *A. clyton texana* in: Barnes and McDunnough, 1913 (Plate II: Fig. 7, "subpallida", male, syntype, d; Fig. 8, "subpallida", female, syntype, d; Fig. 9, "subpallida", female, syntype, v; Fig. 10, "texana', female, v); Holland, 1931 (Plate LX: fig. 6, near "texana", female, d); Pyle, 1981, 1985 (Plate 666L, "texana"?, male, v); Scott, 1986 (Plate 19 [figs.] 142a, male, d; 142b, "subpallida", female, d; 142c, female, v); Stanek, 1977 (fig. 81 [top left], "texana"?, male, d). Photographs of *A. clyton louisa* in: Montgomery, 1984 (pp. 3-4, male, d); Pyle, 1981, 1985 (Plate 661, females, v, d). Howe (1975) ably illustrated individual specimens (Plate 12: fig. 7, near "texana", male, d, v; fig. 8, near "texana", female, d, v; fig. 9, *louisa*, male, d, v; fig. 10, *louisa*, female, d, v; Plate 13: fig. 8, "subpallida", male, d, v; fig. 9, "subpallida", female, d, v).

A. clyton texana and A. clyton louisa limbal spots white, Cu1 with brown ring often expressed. Ground color basally light brownish orange, distally chestnut brown (light yellow-orange posteriorly distally). Browns of A. clyton louisa much darker, but otherwise similar to A. clyton texana. Females tawnier than males.

# Range

A. clyton clyton (Plate 3). Eastern United States and extreme southern Ontario, Canada. Specimens examined (states listed alphabetically and by county; over 850 non-reared adults):

CANADA: Ontario (prov.)

U.S.A.: ALABAMA: Marengo, Tuscaloosa; ARKANSAS: Desha, Madison, Pulaski, Washington; CONNECTICUT: Fairfield, Tolland; FLORIDA: Liberty; GEORGIA: Bibb, Chattahoochee, Richmond; ILLINOIS: Adams, Cook, Macon, Madison; INDIANA: Kosciusko; IOWA: Polk, Woodbury; KANSAS: Douglas, Franklin, Greenwood, Johnson, Labette, Riley; KENTUCKY: Edmonson, Garrard, Jefferson, Nelson; LOUISIANA: Jefferson, Orleans, Rapides (parishes); MARYLAND: Allegany, Baltimore, Washington; MASSA-

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CHUSETTS: Hampden, Hampshire; MICHIGAN: Genesee, Lenawee, Washtenaw; MISSISSIPPI: Chickasaw, Clay, Hancock, Hinds, Holmes, Lauderdale, Lee, Lowndes, Madison, Oktibbeha, Rankin, Warren, Washington, Wilkinson; MISSOURI: Cass, Clay, Jackson, St. Louis; NEBRASKA: Cass, Douglas; NEW JERSEY: Cape May, Essex, Hudson, Hunterdon, Middlesex, Morris, Sussex; NEW YORK: Dutchess, Kings (Long Island), Orange, Queens (Long Island), Richmond (Staten Island), Tompkins, Westchester; NORTH CAROLINA: Durham; OHIO: Champaign, Franklin, Hamilton, Montgomery; OKLAHOMA: Garfield; PENNSYLVANIA; Allegheny, Beaver, Lancaster, Washington; SOUTH CAROLINA: Charleston, Edgefield, Richland; TENNESSEE: Cocke, Davidson, Hamilton, Knox, Lake, Maury; TEXAS: Angelina, Aransas, Bailey, Baylor, Bowie, Burnet, Coryell, Dallas, Harris, Hill, Houston, Limestone, Live Oak, San Patricio, Tarrant, Travis; VIRGINIA: Dinwiddie, Fairfax, Montgomery, Rockbridge, Wythe; WASHINGTON, D. C.; WEST VIRGINIA: Hampshire, Kanawha.

A. clyton flora: Peninsular Florida, coastal Georgia, rarely into south Carolina. Specimens examined (over 250 non-reared adults):

U.S.A.: FLORIDA: Alachua, Broward, Dade, Hendry, Indian River, Levy, Monroe, Nassau, Orange, Palm Beach, Pinellas, Polk, Putnam, St. Johns, Seminole, Volusia; GEORGIA: Chatham, Glynn; SOUTH CAROLINA: Charleston.

A. clyton texana: Northern Mexico, southwestern United States: southern Arizona, western Kansas, western Oklahoma, western Texas. Specimens examined (over 1,150 non-reared adults) [form "subpallida" (°) (over 350 non-reared adults)]:

MEXICO: Chihuahua, Coahuila, Hidalgo,°? Sonora° [states]

U.S.A.: ARIZONA°: Cochise, Pima, Santa Cruz; KANSAS: Barber, Washington; NEW MEXICO: Eddy; OKLAHOMA: Blaine, Childress, Cleveland, Cotton, Garfield, Kiowa, McClain, Woodward; TEXAS: Armstrong, Atascosa, Bailey, Bastrop, Baylor, Bee, Bell, Bexar, Blanco, Bosque, Brewster°, Brooks, Burnet, Comal, Coryell, Dallas, Dimmitt, Goliad, Gonzales, Hays, Jeff Davis°, Kaufman, Kendall, Kerr, Kleberg, Live Oak, Llano, Maverick, McLennan, Medina, Menard, Nueces, Palo Pinto, San Patricio, Tarrant, Terrell, Travis, Uvalde, Val Verde, Victoria, Webb, Wichita, Williamson counties; also Brazos, Cameron (coastal), Harris rarely.

A. clyton louisa: Far south Texas in lower Rio Grande Valley; northeastern Mexico. Specimens examined (over 350 non-reared adults):

MEXICO; Nuevo Leon, Tamaulipas [states]

U.S.A.: TEXAS: Cameron, Hidalgo, Starr counties.

A female specimen labelled, "Texas: Beeville, Bee Co., June-10-1970, W.H. Howe," in the AMNH is *A. clyton louisa*. Perhaps this is a stray or a phenocopy, rather than a mislabelling. A reared male specimen labelled, "Bastrop, 18.VI.62," in the AMNH is probably from Brownsville.

## Discussion

*A. clyton* is not a particularly common butterfly unless its habits are known to the observer. Adult butterflies stay near the host plant. The

egg masses and gregarious larvae are easily found by parasitoids and predators according to Riley (1873). Such an oviposition strategy as depositing eggs in large masses would presumably have been selected for the increased survival of offspring (genetically similar larvae). Larvae have evolved predator avoidance and defensive behaviors.

Several incorrect host records have been reported for this species and for *A. clyton clyton* in particular. For a discussion of these records the reader should consult my dissertation.

A. clyton flora is related to A. clyton clyton just as A. celtis reinthali is related to A. celtis celtis. These taxa of the Florida peninsula have evidently been isolated from the more mainland populations of their respective species. Individuals are larger in size and could be given as examples of "island gigantism" within the genus. Was it during the Pleistocene that populations of these butterflies were isolated in limestone sinks with their host plants? The central peninsula of Florida has been thought to be a refugium during the Pleistocene for a few butterflies (Klots, 1965).

A. clyton louisa is fairly distinct and has only limited zones of intergradation with the similar A. clyton texana. These zones are found on the northern edges of its range, coastally north of Brownsville, and inland, up the Rio Grande above Starr County, Texas. The larvae have dark heads in contrast to their colorful bodies. Adults are progressively darker southward into Mexico. The form "subpallida" of A. clyton texana occurs in the western end of the distribution of the typical form "texana" and is synonymized. On the whole, western populations are lighter in color and have less distinct markings. More field work is needed to determine if either A. clyton louisa in eastern Mexico or A. clyton texana ("subpallida") in western Mexico (northern Sonora where it presumably occurs) overlaps the range of A. idyja argus.

The hymenopterous parasites *Telenomus* sp. and *Tetrastichus* sp. attack eggs of *A. clyton clyton* (Friedlander, 1984). Both tombstone pupae (Clausen, 1940) (Hymenoptera: Eulophidae, *Elachertus* sp.) and the attached banded barrel-shaped cocoons of the ichneumonid wasp *Microcharops tibialis* (Cresson) are frequently found in association with middle instar larvae. Both *Cotesia* and *Meteorus* species (Hymenoptera: Braconidae) have been reared from *A. clyton clyton* larvae. Larvae are presumably attacked by tachinid flies, as other species are. Larvae are also subject to predation by bugs, ants and vespid wasps. The larval parasites *Meteorus* sp. and *Cotesia* sp. have been reared from middle instar larvae of *A. clyton flora* by N. Stamp (det. Friedlander). The whole range of insect parasites and predators that have been recorded for hackbberry butterflies has been reported for members of *A. clyton texana* or *A. clyton louisa* (Friedlander, 1984).

# Asterocampa idyja (Geyer, [1828])

(Genitalia, Figure 7)

Synonymies and discussion of types

# Asterocampa idyja idyja (Geyer, [1828])

?Papilio herse J. C. Fabricius, 1793 (identity obscure; junior homonym of Papilio herse Hufnagel, 1766)

Doxocopa idyja C. Geyer, [1828]; J. Gundlach, 1881 (biology)

Nymphalis idyja, D. F. Poey, 1847

Apatura idyja, (E. Doubleday), et al., (1850)

Apatura idyia, W. H. Edwards, (1873) (misspelling)

Apatura clyton, W. F. Kirby, 1871 (part)

Apatura herse, H. Strecker, 1878

Chlorippe idyja, W. F. Kirby, 1901

Doxocopa idyja padola H. Fruhstorfer, 1912

Asterocampa lycaon from idyja, J. Röber, 1916; D. M. Bates, 1935

Asterocampa clyton idyja, H. Stichel, 1938

Asterocampa clyton padola, H. Stichel, 1938

Asterocampa argus idyja, W. P. Comstock, 1944

Asterocampa idyia, N. D. Riley, 1975 (misspelling)

Asterocampa idyia form padola, N. D. Riley, 1975 (misspelling)

Asterocampa lydia, E. Welling, 1981 (misspelling!)

The type of *Doxocopa idyja* is presumed to be lost. It is represented by figures 3 and 4 of plate [13] in (Hübner, J. and) C. Geyer, 1826-1841 [1828], *Sammlung exotischer Schmetterlinge*, 3 (Hemming, 1937). Figure 3 is of an adult female in dorsal view with well defined postmedian spots in the FW and ocellate limbal spots in the HW. Figure 4 is a ventral view of a well marked adult female. There is no surviving manuscript description accompanying the plate. The illustrations are to be considered as representing the type.

The holotype of *Doxocopa idyja padola* is in the Staudinger collection housed in the ZMHU in Berlin and has been examined. The description is based on the male which exhibits a greater degree of orange scaling than does the illustration of *D. idyja*. It is from an unspecified location in Haiti ("Haiti, 25/10 96. Hopke" "*Doxocampa* [sic], *idyja padola*, Fruhstorfer" "Typus" "Zool. Mus., Belin"). A specimen of *A. idyja idyja* has recently been collected on the northern coast of Haiti (Nord: Cormier Plage) (Schwartz, 1983) and others have been taken near Cap-Haitien. Specimens from many other localities on Hispaniola (in the Dominican Republic) fill out the known range of color variation of this subspecies.

# Asterocampa idyja argus (H. W. Bates, 1864)

Apatura argus H. W. Bates, 1864
Doxocopa argus, F. D. Godman and O. Salvin, (1884)
Apatura ([=|Doxocopa) argus, O. Staudinger (and E. Schatz), (1888)
Doxocopa argus form armilla H. Fruhstorfer, 1912 (excluded name)

Asterocampa argus, J. Röber, 1916; C. C. Hoffmann, 1940 Asterocampa argus from armilla, J. Röber, 1916 (excluded name) Doxocopa idyja var. argus, A. Hall, 1916 [1983] (microfiche)

The type specimen of *Apatura argus* (Bates) is in the BM(NH) (Godman and Salvin, 1884; Gabriel, 1927; Stichel, 1938). This holotype is a male from the Motagua Valley [El Progresso; Lamas, pers. comm.] in Guatemala ("Motagua, valley" "Apatura, argus, Bates" "[male]" "Type, H. T." "Type., Sp. figured." "Motagua, Valley., F. D. G. & O. S." "B. M. TYPE, No. Ph. 9126., Apatura, argus, [male] Bates." "B. C. A. Lep. Rhop., Doxocopa, argus, Bates., Godman-Salvin, Coll. 1916-4.").

Doxocopa argus form armilla, based on 2 females (Hannemann, pers. corr.), is a color form and not representative of a geographically or genetically isolated population. Fruhstorfer (1912) and Röber (1916) indicated that specimens of both sexes exhibited the band. It is the typical and more common form of A. idyja argus found throughout the range of this subspecies. The lectotype (designated here) is in the ZMHU, Berlin. It is from Honduras ("Hond., Wittk." "Doxocampa [sic], argus armilla, Fruhst." "Typus" "Zool. Mus., Berlin"). I have not seen the paralectotype. I have not yet found any reference to "armilla" that uses this excluded form name as a subspecies name (potentially validating the name).

## **Diagnosis**

A. idyja idyja is separated from A. idyja argus best by its geographic location in the Greater Antilles. Not enough is known about the immature stages to differentiate these stages from A. idyja argus, but preliminary studies of fifth instar larval head capsules and pupal cases indicate near morphologial identity. At least some, and perhaps all, individual larvae of A. idyja idyja have less pigmented head capsules than those of A. idyja argus. A idyja idyja adults resemble the dark forms of both sexes of A. idyja argus but are more subdued in color and somewhat smaller in size. I know of no adults of A. idyja idyja exhibiting the characteristic post-median band of the FW found in the light form of A. idyja argus.

A. idyja argus is most easily differentiated from A. idyja idyja by its geographic location in Central America (including Mexico). The adults of A. idyja argus are slightly larger and more brightly colored. In addition, most specimens are of the light form, the postmedian spots of the FW expanded and forming a narrow golden (yellow) band across the discal area similar in appearance to the pattern found in a number of other butterflies in Central America and Mexico.

# Descriptions of life stages

Gundlach (1881) provided brief descriptions of the mature larva and pupa of *A. idyja idyja*. All of the immature stages of *A. idyja argus*,

except the first and second instar larvae, are desribed in Friedlander (1986a).

## EGGS AND EGG DEPOSITION:

Egg of *A. idyja idyja* presumably of Clyton group type, deposited in masses. Egg of *A. idyja argus* typical of Clyton group, 19-20 ribs, 0.8 mm wide by 0.9 mm high, deposited in large clusters (300  $\pm$  eggs). Micropylar rosette with 66-8 petals.

### LARVAE:

Larva of A. idyja idyja typical of Clyton group, with variably black head and anal horns, body striped with yellow and green. Lightly pigmented larvae, with mostly green heads and green anal horns, are known.

Mature larva of *A. idyja argus* of Clyton group type, 3-4 cm long, head and body (maximum) 5 mm wide; anal horns short, each 1 mm long. Head capsule black, hairy, with whitish patches on lower face and posteriorly on antlers. Mandibles with a single cutting edge. Body integument studded with white chalazae bearing short colorless setae. Spiracles whitish. Body longitudinally striped with shades of yellow and olive green with black anal horns. Heart-line black. Subdorsolateral band greenish black with olive center; spiracular band olive green with intermittent yellow center; prolegs and venter olive green. Subdorsal, supraspiracular and subspiracular bands light yellow. Olive green line separates inner subdorsal band from outer (dorsolateral) band. Intensity of yellow in bands varies.

Third and fourth instar larvae do not differ in any major way from mature larvae except in size; earlier instar larvae not yet described.

## PUPAE:

Pupa of A. idyja idyja green, similar to that of A. idyja argus.

Pupa of A. idyja argus typical of Asterocampa, 2.1-2.6 cm long, 0.7-0.9 cm wide, 0.9-1.2 cm high at abdominal crest (third segment). Pupa yellowish green with whitish markings on head and body carinae. Diagonal white stripes on sides of abdominal segments 2-7 between crest and spiracles, higher ends posterior. Head prolongations blunt. Metanotum very short medially (longitudinally). Anterior median edges of third through eighth abdominal segment produced into spines, subtended by pairs of black spots. Length of cremastral bed of hooks 3.5-4.1 mm.

### ADULTS:

Antennae of A. idyja idyja (Pl.22, figs. G-I) brown above, with white tufting at lateral bases; front tan above, white below; pair of white tufts mesal to chaetosemata; palps brown above, white below, tan mesally; occiput scaling white laterally (seen as 2 lateral dots from above). Body light brown, orange brown above, light tan below; femora 2 and 3 darker dorsally, tibiae and tarsi 2 and 3 tan, as are foretibiae mesally; tan to brown posteriorly, to genitalia. Body above same color as basal ground color of HWs, but black color of cuticle shows inbetween scaling. Vertex and patagia same color as costal cell of FWs. Costal FW length (Fig. 4) of A. idyja idyja 24.0-29.0 mm (males,  $26.3 \pm 1.5$  mm, n = 8), 34.0-37.0 mm (females,  $35.0 \pm 10$  mm, n = 7). Male genitalia (Fig. 7E): long aedeagus (5.0-5.5 mm) and saccus (3.8-4.5 mm). Valves 2.2-2.3 mm long; uncus bilobed with deep notch, as in A. idyja argus. Terminal tuft composed of straight hair-scales dorsally on intersegmental membrane 8-9. Female genitalia: long,

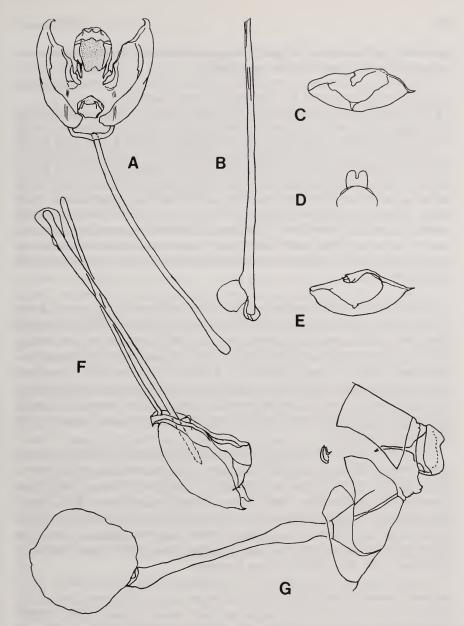


Fig. 7. Genitalia of Asterocampa idyja (Geyer).

Male genitalia:

Whole genitalia (**A**, ventral view, valves spread) with aedeagus (**B**) separate: Honduras, no date, CMNH. TF gen. prep. no. 1982-23. *A. idyja argus* (Bates).

Right valve (**C**, mesal view) and uncus (**D**, ventral view):: Mexico: Oaxaca, 2.1 mi. nw. Totolapan, July 1981, reared, T. Friedlander. TF gen. prep. no. 1982-1. *A. idyja argus*.

Right valve (**E**, mesal view): Cuba, no date, CMNH. TF gen. prep. no. 1982-2. *A. idyja idyja*.

Whole genitalia (F, left lateral view): Honduras, no date, CMNH. TF gen. prep. no. 1982-23. *A. idyja argus*.

Female genitalia:

Whole genitalia (**G**, left lateral view): Mexico: Veracruz, Jalapa, no date, CMNH. TF gen. prep. no. 1982-48. *A. idyja argus*.

sclerotized ductus (3.8 mm) adjoining large ostiolar funnel. No signum observed on corpus bursae. Anal papillae emarginate.

A. idyja idyja figured in Comstock (1944: Plate 7, Figure 9). Male in dorsal and ventral view illustrated in N. D. Riley (1975: pl. 4, fig. 3).

FWs dorsally with basal ground color tawny (medium brown scales mixed with orange ones, with more orange anteriorly in the discal cell); discal cell with 2 bars, close together, the more basal one obscure, indicated with dark brown scaling, almost separated into 2 separate spots, the more apical one dark brown, at end of discal cell; apical ground color dark brown (medium dark to dark brown scaling), interrupted by lighter marginal and submarginal bands, and 5 white limbal spots (R5 to Cu1); veins brown; pale yellow-orange postmedian spots nearly alligned in slight zigzag (R5 to A1); fringe dark brown with white centrally in cells R3 to Cu2+A1. Variation: amount of brown scaling increased, infuscating base of wing; postmedian spots reduced in size in females; orange scaling in discal areas increased; cell M2 with yellow-orange spots just beyond apical discal bar.

Hws dorsally with ground color tawny, infuscated by brown hair-scales, light grayish brown scales in anal cup; discal markings virtually obscured; limbal spots dark brown, surrounded by orange-yellow scaling (R5 to A1), some with whitish pupils (Cu1); veins brown; submarginal, marginal bands, fringe (Sc+R1 to Cu2-A1) as in FW. Variation observed in orange scaling surrounding eye-spots (increased), infuscation increased, eye-spot size decreased, number of eye-spots with pupils increased; males with more orange surrounding eye-spots, females with rings only (ocellate).

Wings ventrally with patterns of dorsal side repeated in lighter tones; apical area of FW and all of HW washed with tan scaling; veins brown. FW basally, below discal cell, grayish to reddish brown, discal bars concolorous; postmedian spots large, virtually confluent; FW limbal spots white. HW limbal spots dark brown with large whitish blue pupils, surrounded by yellow rings inside orange to brown edging. Variation observed included browns replaced by light orange. HW limbal spots not expressed (R5, M2, M3) in some females.

A. idyja argus (Pl.22, figs. J-O): Antennae dark brown above, each segment dorsally with black scaling terminating in brown; front light brown above, white below; palps medium brown above, white below, light brown mesally, occiput scaling white laterally. White tufting at lateral bases of antennae and mesal to chaetosemata. Body color above brown, black coloration of cuticle showing through, with a few orange scales mixed (same as HW basal ground color); patagia hair scales same as FW costal cell, but strap scales light brown with white mixed. Body ventrally light brown, becoming darker posteriorly. Legs tan. Costal FW lengths (Fig. 4) 28.0-31.0 mm (males, 29.1  $\pm$  1.2 mm, n = 18), 34.0-40.0 mm (females, 36.9  $\pm$  1.8 mm, n = 11). Male genitalia (Fig. 7A-D, F): long saccus (4.3-5.5 mm) and aedeagus (5.5-6.9 mm). Valves 2.2-2.6 mm long; uncus with 2 rounded lobes separated by deep notch. Dorsal tuff of

hair-scales on membrane 8-9 straight. Female genitalia (Fig. 7G): long, sclerotized ductus (4.6 mm) joining large ostiolar funnel. Anal papillae emarginate.

Only published figures of A.  $idyja\ argus$ , to my knowledge, in  $Biologia\ Centrali\ Americana$  (vol. 38, Godman and Salvin, 1879-1901 (1884), Pl. 30, figs. 12, 13 (male), 14 (female)) and in Seitz (ed.),  $Die\ Gro\beta schmetterlinge\ der\ Erde$  (vol. 5, Röber, 1907-1924 (1916), Pl. 109 (male)).

Dorsal FW with basal ground color bright tawny (orange and brown scaling mixed); discal bars faint, brown, close together; distal ground color dark brown (almost black); veins brown basally, darker apically; limbal spots white (R5 to Cu1); orangish yellow postmedian spots typically enlarged, those in R5 and M1 joined with similarly colored spots beyond apical discal bar, the whole effect being a "golden" band dividing wing (tawny basally and black apically); "dark from", postmedian spots separate as in A. idyja idyja, submarginal and marginal bands extremely faint apically, becoming lighter (yellow-orange) at tornus, merging with band in typical from) fringe dark brown with white centrally in cells R3 to A1 (or Cu2+A1). Variation: frequency of dark form, black fades in museum specimens, amount orange scaling.

HW dorsally with ground color tawny infuscated with brown obscured by grayish brown hair-scales basally; anal cup grayish brown; no indication of discal bars or postmedian spots; veins brown; limbal spots dark brown (R5 to Cu2) surrounded by ring (females and dark males) or block (normal males) of orange scaling; submarginal and marginal bands orange typically to grayish or reddish brown (dark form); fringe as in FW, but with wider white rows of scales.

Wings ventrally with same pattern as dorsal side, but lighter. Tan scaling in apex of FW and throughout HW; veins, discal markings and subtending line of postmedian spots in HW brown. Variation: size of ocelli in limbal HW spots, amount of lighter tan scaling, amount dark brown in Cu1 limbal spots FW (ringedness), thickness of postmedian band FW (base of cell M3 good measure), washing out of HW (females, Rs).

# Range

A. idyja idyja (Plate 4): Great Antilles — Cuba, Isle of Pines, Hispaniola, Puerto Rico. Localities of specimens examined (over 100 non-reared adults):

CUBA: Granma, Guantanamo, Habana, Isla de Pinos, Pinar del Rio, Santiago de Cuba [provinces]

HISPANIOLA: Haiti (Nord, l'Ouest), Dominican Republic (Altagracia, Barahona, La Romana) [countries (provinces)]; PUERTO RICO: Coamo Springs, San German, Salinas, Quebradillas [cities].

A. idyja argus (Plate 4): Mexico, Guatemala, Honduras, Nicaragua (possibly El Salvador, Belice; not known from Costa Rica, Panama,

Colombia, southward). Localities of specimens examined (over 150 non-reared adults):

MEXICO: Chiapas, Guerrero, Hidalgo, Jalisco, Michoacan, Morelos, Nayarit, Oaxaca, Puebla, San Luis Potosi, Sonora, Tamaulipas, Veracruz [states]

HONDURAS: San Pedro Sula [city] GUATEMALA [no locality given]

One should expect *A. idyja argus* to be found also in Sinaloa, Colima, Mexico, Tlaxcala, and potentially Nuevo Leon and Tabasco in Mexico, where tree-like *Celtis* species grow. Specimens reported (as labelled) from Bogota, Colombia are in reality from Honduras, the faded original labels having been replaced with the erroneous locality label. This butterfly's range is apparently limited by its host plants (and habitat destruction). *Celtis schippii* Trel, ex Standl. needs to be investigated as a possible host of the subspecies in the wetter areas of Central America.

### Discussion

The type specimen of  $Doxocopa\ idyja$  was part of a collection from Cuba sent to Hübner about a decade earlier than plate [13] was published. The plate was probably drawn before 1823 when figures of other specimens from Cuba were published (such as those of Lucina [sic] sida and  $Siderone\ nemesis$ ).

A. idyja idyja is found along river systems coastally where its food plant, *Celtis trinervia*, grows. The butterfly must now be considered to be rare due to habitat destruction over most its range. The immature stages need to be rediscovered and described thoroughly.

The literature record of *Ardisia* as a larval host plant (e.g., Riley, 1975) is probably the result of either misinterpretation or misidentification. In the description of the immature stages of *A. idyja idyja*, Gundlach (1881) stated that he was not entirely sure of his plant identification ("La oruga viva sobre un arbol, *que creo sera* el Agracejo de sabana (Ardisia cubana)," italics added). Möschler (1890) repeated the record without comment that the larva was found on *Ardisia*. W. P. Comstock (1944) cited Gundlach and added that a number of specimens of *A. idyja idyja* had been reared in Hispaniola on a species of *Celtis*. This rearing was mentioned again in Brown and Heineman (1972). A few cast larval and pupal skins are in the AMNH, and the latter are on *C. trinervia* Lam.

A. idyja idyja remains the least well known hackberry butterfly. The sometimes black head and anal horns of the late instar larvae noted by Gundlach (1881) and the short metanotum of the pupa are diagnostic for A. idyja. The larval body is striped like some eastern larval populations of A. clyton but tends to have more intense shades of yellow and green (olive). N. D. Riley's (1975) abbreviated description of the mature larva, preseumably based on Gundlach's article, is in error in stating that the larvae have orange (instead of yellow, "amarilla" in Gundlach) longitudinal body stripes.

A. idyja argus has been recorded from Celtis caudata Planch. (Friedlander, 1986a) in southern Mexico. C. reticulata Torr. is used as the host plant in northwestern Mexico and C. laevigata Willd. is used in northeastern Mexico. C. trinervia should be the host in Central America These trees grow along streams and rivers and on limestone outcrops in seasonally dry lowlands. Species in the Momisia-group of hackberries are not considered suitable hosts. Possible reasons for their unsuitability include chemical differences between these and other plants in the genus, microhabitat differences in temperature in which the plants are found, and differences in the size and architecture of the plants. Unless Celtis schippii proves to be unsuitable as well, there is no obvious reason for A. idyja argus not to be found farther south than it has been. Lamas (pers. comm.) confirms that the butterfly has not been found in South America.

One of the more interesting features of A. idyja argus is its light form ("die Armspange" as Fruhstorfer (1912) put it). Many other nymphaloid butterflies within the range of this subspecies share this wing pattern. Notable among these are species of Smyrna (especially females), Historis, Hypanartia and the brassolid genus Opsiphanes. The high percentage of light individuals in the southern part of the range of A. idyja argus may well be due to selection for the mimetic resemblance. It is not known if populations occurring in Sonora or Tamaulipas have dark form females. Dark females, apparently more common in Central America, resemble the crepuscular Pycina zelys, a tropical nymphalid. The latter color form also occurs in A. idyja idyja.

How did this species become distributed across the Greater Antilles, Mexico and Central America? Was a barrier crossed to attain the island/mainland distribution or did the butterfly's range once span the two (by land bridge or pre-drift) and then become disjunct? In which area did the butterfly originate? The phenotypic appearance of *A. idyja idyja* shows the strongest resemblance to that of *A. idyja argus* from Central America. What evidence there is to support one hypothesis over another will be presented in the next section.

Scelionid parasites of eggs (*Telenomus* sp.) have been reported (Friedlander, 1984) from a clutch found in Oaxaca.

# PHYLOGENY AND BIOGEOGRAPHY OF HACKBERRY BUTTERFLIES

The hackberry butterflies have been recognized as constituting a natural group for 100 years (Godman and Salvin, 1884; Barnes and McDunnough, 1912). They were given their valid name *Asterocampa* by Röber in 1916. No published revisions of the genus have appeared since the last date.

Hackberry butterflies are in the Apaturinae (Stichel, 1938). This subfamily of butterflies is poorly defined (Niculescu, 1965) but its

members do share a number of traits, some of which might be interpreted as synapomorphies. DeVries *et al.* (1985) place the apaturines near the base of the nymphaloid phylogenetic tree on the basis of mostly larval characters analyzed cladistically.

The application of cladistic methodology to butterfly classification has been successful, especially as applied to higher taxa (nymphaloids, DeVries *et al.*, 1985; higher taxa of Papilionidae, Hancock, 1983; genera of Parnassiinae, Hiura, 1980; families, Kristensen, 1976). Phylogenetic revisions of butterfly genera have also been published (Ackery and Vane-Wright, 1984; Hiura, 1981; Jong, 1978; Smiles, 1982). An early review of cladistic classification as applied to Lepidoptera is given by Nielsen (1979).

## PHYLOGENY:

Adult apaturine butterflies, as well as several satyrid, nymphaline and charaxine butterflies, were studied for shared derived characters (synapomorphies). References on the morphology and biology of the other life stages of these butterflies were searched, in cases in which specimens were not available for study. Detailed morphological work was carried out on all life stages of the hackberry butterflies and character states compared with those found in other apaturines (outgroup comparisons). Characters found to be useful in the construction of a hypothesized phylogeny of hackberry butterflies are discussed in this revision.

Two-state characters investigated for the life stages of hackberry butterflies selected to constuct the cladogram in this section are listed in Table 9. Each is discussed with regard to the distribution and polarity of its character states. The polarities of characters are largely hypothesized by out-group comparison, as shown in the table.

The sister group to the Apaturinae, which is certainly among the nymphaloid butterflies, is not yet recognized. Many different nymphaloids were examined in an effort to hypothesize synapomorphies which might define the subfamily can be viewed as symplesiomorphies (indistinct antennal club, open discal cells, larvae without body scoli), or if they are apomorphic, the character states recur within the Nymphaloidea, and the characters are not necessarily synapomorphies. Several characters (host plants, larval head morphology, adult genitalia and wing pattern) were found to have merit in defining the Apaturinae.

GENITALIA: Le Moult (1950) and Niculescu (1965) recognized that the long aedeagus and saccus of male genitalia serve to define the Apaturinae. I agree with their views.

HOST PLANTS: A wide variety of angiosperms are used as larval hosts for nymphaloid butterflies (Ackery, 1984). Apaturines use only a small number of plant genera confined to (possibly) four plant families: Betulaceae (Ostrya), Fagaceae (Quercus), Salicaceae (Populus, Salix) and Ulmaceae (subf. Ulmoideae: Trema, Ulmus, Zelkova; subf. Celtidoideae: Celtis, Gironniera).

Graeser (1888) reported that Mimathyma schrenckii (Menetries)

pupae were on *Ostrya* and the *Mimathyma nycteis* (Menetries) larvae lived on *Ulmus*. No further reports confirm these findings. *Sephisa dichroa* (Kollar) has been cited as using *Quercus incana* Roxb. (Fagaceae) as its larval host (Mackinnon and de Niceville, 1897; Moore, 1899). That their host is an oak seems unlikely, and even Moore's illustrations of larvae and pupae show them associated with a *Celtis*-looking host. Recently, Görgner (1984) published the host plant of *Euapatura mirza* Ebert as *Zelkova crenata* Spach, but his photographs indicate (as judged by the pinnipalmately veined leaves) that the host is a species of *Celtis* (or possibly that *Z. crenata* is misclassified?).

The Salicaceae (Salicales) are unique among the Dilleniidae in many characters, but are thought by most authors to be closest to the Violales. Fossils belonging to Salix have been found dating to the Eocene of North America (Cronquist, 1981). Both Salix and Populus are widespread, but they are not found in the Indoaustralian biogeographic realm. Only one genus of Apaturinae, Apatura, is known to use Salicaceae as larval hosts.

Other nymphaloid taxa using Salicaceae include some Limenitini and Nymphalini. Some Argynnini and a few Charaxinae feed on members of the Violales (Ackery, 1984; Smart, 1977).

Chemical studies by Giannasi (1978) and palynological data (Zavada and Crepet, 1981) on ulmaceous genera support Grudzinskaya's (1967) conclusions that the celtidoids form a distinct group from the ulmoids. Cronquist (1981) cites Grudzinskaya's feeling that perhaps the Celtidoideae are closer to the Moraceae than the Ulmaceae. The Ulmaceae belongs with the Barbeyaceae, Cannabaceae, Moraceae, Cecropiaceae and Urticaceae in the Urticales (Hamamelidae) (Cronquist, 1981).

Other nymphaloid taxa having Celtidoideae as larval hosts include the Libytheinae and *Polygonia*-like Nymphalini. Other nymphalines (e.g., Coloburini, Marpesiini), Calinaginae, and some danaines feed on Cannabaceae, Cecropiaceae, Moraceae, or Urticaceae (Ackery, 1984; pers. obs.).

It is my feeling that the sister group of the Apaturinae will be found among those butterflies using Urticales as larval hosts. The apaturine butterflies appear to have specialized early on only the Celtidoideae of the Ulmaceae, while other nymphalines which might be considered as possible sister groups and which use Ulmaceae as larval hosts feed on the Ulmoideae genera as well. Within the Apaturinae I think the Celtidoideae are the primitive host plants (Celtidoideae as larval hosts would be a synapomorphy for the Apaturinae). With this view the use of Salicaceae is an advance, perhaps a synapomorphy for *Apatura*, just as *Quercus* would be for *Sephisa*.

LARVAL HEAD MORPHOLOGY: Many nymphalöid caterpillars have antlers at the vertices of the head capsule (e.g., Müller, 1886; also, DeVries *et al.*, 1985). Apaturine caterpillars have antlers which are bifurcate at the tips. Each antler has a small number of subordinate scoli in definite patterns. Apparent specializations in other nymphaloid groups having antlers include terminal antler clubs or spikes, the latter

often accompanied by a subtending rosette of scoli. Antlers found among the Marpesiini are highly elongate and curved. The primitive pattern for apaturines and their closest relatives would apear to be like that shown by the antlers of *Calinaga*, which are moderately long, straight, blunt and warty, with each wart supporting a seta. Various warts could then be modified into subordinate scoli. The basic pattern for Apaturinae is, I believe, shown by the antlers of *Sasakia* (see: Shirozu and Hara, 1979).

WING PATTERN: There is an apparent dominance of limbal spot Cu1 in the forewing of apaturine butterflies. The basic nymphaloid wing pattern of concentric rows of spots and bands described by Schwanwitsch (1924) and Süffert (1929) and modified by Nijhout (1978, 1980a) and others, is used here as a starting point for evaluating such evolutionary modifications. One modification of this primitive design found in apaturine (and just a few other nymphalid butterflies, e.g., *Baeotus*, *Cyrestis*, *Kallima*) is the retention of limbal spot Cu1 (various losses in expression of the other limbal spots), especially in the forewing.

This pattern might represent a synapomorphy for the Apaturinae, or alternatively, a symplesiomorphy, if those other nymphalines share the trait inherited from a common ancestor.

One notion strikes me when thinking about the Apaturinae. There seems to be a natural division between those genera which exhibit blue iridescence and those which do not. Blue iridescence might well be a symplesiomorphy in the Apaturinae.

Within the Apaturinae there are a few discernable clades. Of immediate interest in this revision are the hierarchical clades containing *Asterocampa*. Three characters, pattern of scoli on larval head antlers, form of pupal cremaster, and male genitalia, are useful in discussing these hypothesized clades.

The number and position of basal subordinate scoli on the antlers among apaturine larvae is variable. There appears to be a basic pattern of a few scoli in vertical rows on the antler below the terminal pair (forked tip of antler). In various lines within the Apaturinae different sets of subordinate scoli are emphasized or suppressed. In the line leading to Asterocampa many scoli are suppressed, leaving only five basal scoli and the terminal pair subtended posteriorly by a single scolus. This pattern is apparently shared only by Chitoria, Dilipa and Euapatura, and possibly, Thaleropis, but because the larvae are not known to the author for a few of the other apaturine genera, there is reason to suspect some of the other genera as sharing this condition as well.

A smaller clade within the first might be defined by *Chitoria* and *Asterocampa*, which appear to share a pupal synapomorphy. These are the only 2 apaturine genera known to have a greatly elongated cremastral pad (Edwards, 1878b; Muroya *et al.*, 1967; Riley, 1880). The cremastral hooks extend in a "Y"-shaped pad anteriorly to the level of the sustainers.

Looking at *Asterocampa* for possible synapomorphies turned up only one morphological character which might serve to define the genus. A survey of the morphology of the uncus of apaturine male genitalia revealed that only *Asterocampa* has a broad, bilobed uncus, whereas all the other genera investigated, including *Chitoria*, have an elongate, narrowed and pointed uncus.

One of the more striking features of *Asterocampa* as compared with other apaturine genera is its retention (or re-expression) of fully developed eye-spots, particularly on the undersides of the hindwings. This feature is perhaps best viewed as a symplesiomorphy. It could also represent the derepression of expression of these spots, in which case, the character might be viewed as synapomorphic.

The geographic distribution of apaturine genera may be used with caution as a multi-state character or as an independent set of biogeographic characters with which to test area relationships against morphological relationships. Considering the former, Asterocampa is the only extant Nearctic apaturine genus. The shale fossil apaturine (?!) butterfly from the Late Oligocene of Florissant, Colorado, Chlorippe wilmattae Cockerell (1907), occurs with fossil Celtis (Lamotte, 1952), establishing the presence of such butterflies in North America at a time consistent with one hypothesis for the arrival of the ancestors of hackberry butterflies. Members of the Neotropical genus Doxocopa are invading North America at the present time, and probably had done so prior to the Pleistocene. The geographic position of hackberry butterflies is considered by me to be apomorphic relative to Chitoria and all the other apaturine genera which are Old World in distribution (I think Doxocopa is a South American, Southern Hemisphere, endemic genus). Colonization of North America from eastern Asia could well have been the first step in the evolution of Asterocampa.

Next, the characters listed in Table 9 will be discussed. These characters are the basis of the hypothesized relationships among hackberry butterflies. Characters are first examined by the technique of Wagner Network analysis and a Wagner Tree is produced by rooting this network of taxa. Cladistic methodology is then applied by hypothesizing synapomorphies among the polarized characters, and the resulting cladogram compared to the Wagner Tree. Apparent homoplasious characters and synapomorphies are discussed in relation to sister group pairs in the cladogram. Finally, a phylogeny of the hackberry butterflies is hypothesized based on this character set.

- 1. The chorion between the longitudinal ribs of the eggs is smooth to quite wrinkled in hackberry butterflies. There is no apparent reason to conclude that wrinkling is the derived condition other than the observation that eggs of other Apaturinae (admittedly, these have not been extensively studied) are not known to have this condition. *Euapatura mirza* Ebert (Görgner, 1984) eggs might have this condition. Only the Celtis group of *Asterocampa* exhibits wrinkling.
  - 2. Aeropyles normally occur along the entire length of the exposed

Table 9. Distribution of character states among hackberry butterfly taxa relative to other Apaturinae.

Characters EGG:	States	LEI	ANT	CEL	REI	TEX	LOU	CLY	FLO	ARG	IDY	OUT-GR
1. sculpturing	smooth chorion between ribs wrinkled chorion between ribs	- ×	- ×	_ ×	- ×	× -	× -	× -	× -	× -	× _	most some?
2. aeropyles	whole length of ribs lacking basally on ribs	× -	× -	× -	× -	- ×	_ ×	 ×	- ×	- ×	- ×	all? none?
3. clutch size	small (1-50), rarely structured large (50-500), structured	× -	× -	× -	× -	- ×	- ×	- ×	- ×	- ×	- ×	most few
4. host plant	Nearctic Celtis Celtis pallida (Neotropical)	- ×	×	× -	×	× -	×	×	× -	× -	× -	other Celtis,etc.
LARVA:												
5. head horns	AB5 of antler>(1/2)L1 AB5 of antler≤(1/2)L1	- ×	- ×	×	- ×	× -	× -	× -	× -	× -	× -	most some
6. body pigmentation	lines and crenations only additional longitudinal bands	× -	× -	× -	× -	× -	- ×	- ×	- ×	- ×	- ×	most some
7. feeding behavior	not gregarious as early instars gregarious as early instars	× -	× -	× -	× -	- ×	- ×	- ×	- ×	- ×	- ×	all? none?
PUPA:												
8. thorax	metanotum>abdomen 1 metanotum <abdomen 1<="" td=""><td>× -</td><td>× -</td><td>× -</td><td>× -</td><td>× -</td><td>× -</td><td>× -</td><td>× -</td><td>- ×</td><td>- ×</td><td>most some</td></abdomen>	× -	- ×	- ×	most some							
9. abdominal keel	anteriorly sharp anteriorly blunt	- ×	- ×	- ×	- ×	× -	× -	× -	× -	× -	× -	some most
10. cremaster	elongated to sustainers not reaching sustainers	- ×	× -	× -	×	× -	× -	×	× -	× -	× -	Chit. most
ADULT (Wings):												
11. discal bars	basal bar solid basal bar forming 2 spots	× -	- ×	_ ×	- ×	× -	× -	× -	× -	× -	× -	most some
12. postmedian spots	M2 beyond M3 M2 and M3 adjacent	× -	× -	× -	× -	×	× -	× -	× -	- ×	- ×	some many
13. limbal spots (FW) [multi-state]	M1, M3 and Cu1 eyespots M3 partially expressed	×	×	- ×	– ×	- ×	- ×	- ×	- ×	- ×	- ×	few few
14.	M1 partially expressed	_	_	_	_	×	×	×	×	×	×	few
15.	Cu1 without pupil	-	-	×	×	×	×	×	×	×	×	some
16.	A2 present	×	_	×	×	_	-	-	_	_	_	none
ADIII m /m · · · · ·	A2 absent	-	×		-	×	×	×	×	×	×	all
ADULT (Terminalia):												
17. anal brush (males)	straight recurved	×	×	- ×	- ×	×	×	- ×	×	×	×	some
10		_	_			-	-	×		_	-	none
18. uncus (m)	broadly notched narrowly notched	×	×	×	×	- ×	_ ×	- ×	- ×	- ×	_ ×	none few
19. valve/saccus (m)	v/s~0.7	×	×	×								
15. varve/saccus (III)	v/s≤0.7	_	_	_	× -	×	×	_	×	×	_ ×	some most
20. valve/aedeagus (m)	v/a >0.65		×	×	×	_	_			_	_	some
- vi varo dodetagao (m)	v/a ≤ 0.45		_	_	_	_			_	×	×	many
GEOGRAPHIC RANGE:	western N. America	×	×	_		×	×		_	×	_	
	estern N. America	-		×	×	-		×	×	-	-	
	peninsular florida	-		×	×	-	-	-	×	-	-	
	Central America Greater Antilles	_		_	-	-	_	-	_	× -	×	

longitudinal ribs of the eggs. The position of the aeropyles corresponds with the ends of the ladder-like horizontal costulae found between the ribs. Aeropyles are absent on the lower halves of the ribs only in the Clyton group of *Asterocampa*.

3. The number of eggs in a clutch ranges from 1 (deposited singly) to well over 500 in a mass for hackberry butterflies. Not many butterflies, and few apaturines, deposit their eggs in distinct clusters consisting of hundreds of eggs. The most space-saving packing design for spherical units such as these eggs approximate is tetrahedral. The behavior necessary for stacking eggs in such a uniform design is more complex than that necessary to place eggs more randomly, whether in piles or

singly. Even though members of some populations of the Celtis group of *Asterocampa* are known to deposit fairly large clutches, the eggs are not strictly tetrahedrally packed as they are in masses deposited by females in the Clyton group. There are few reports of egg depositing behavior in other Apaturinae.

A character correlated with large clutch size is oviposition on mature (old) leaves. This character sate is tentatively considered a derived character state. From the viewpoint of leaf toughness new leaves are both thinner and less tough than old leaves, providing more suitable food for early instar larvae. Chemistry (toxins, deterrents) and nutrition obviously enter into the determination of host suitability. New leaves were found to sustain maximal growth of all hackberry butterfly species in early instars so that there would appear to be no outstanding palatability problem in *Celtis* other than toughness. Early instar larvae of the Clyton group feed gregariously on old leaves and so appear to have made this great food resource available, whereas single larvae are apparently unable to sustain growth on old leaves (personal observations on larvae of both A. clyton and A. celtis). However, there could be a complicating factor to the interpretation that individual larvae are unable to sustain growth on old leaves if behavioral problems arise due to isolation of a gregarious feeder from external cues from its normal feeding partners (Kalin and Knerer, 1977). It is also possible that placement of the eggs on old leaves away from the tips of branches is a means of avoiding egg parasites, which is especially important when virtually all the eggs of a single female are in one place. Female choice of mature trees only as suitable oviposition sites is viewed as a behavioral restriction. Clyton group females generally do not place eggs on juvenile or small trees in spite of apparently suitable food being there.

- 4. Neotropical *Celtis*, subgenus *Momisia*, is thought to be colonizing northward into the ranges of hackberry butterflies. There are both structural and chemical differences between Nearctic and Neotropical hackberries. Subsequent adaptation by some populations of butterflies for usage of these plants as larval hosts is considered to have been a major evolutionary step in the evolution of *Asterocampa*. *A. leilia* has specialized on one species of Neotropical hackberry, *Celtis* (*Momisia*) pallida, and has at present not been successfully reared on any other species of hackberry. The phylogeny of *Celtis* worldwide has not been hypothesized. Most other Apaturinae feed as larvae on species of *Celtis*.
- 5. The lateral scolus AB5 of the antlers extends the lateral frill of head scoli up onto the antlers. This condition is not found in the Celtis group of *Asterocampa*, where AB5 is rather short or vestigial, separating the antlers from the lateral frills. The reduction of scoli on the antlers enhances crypsis and is tentatively considered to be a derived condition. If true this condition is an easily achieved autapomorphy and might well have occurred many times within the Apaturinae.

Antler length is also involved. Short antlers are rarely found among

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apaturine nymphalids. Stouter, shorter antlers are found in the Clyton group of *Asterocampa*. This condition is viewed as a possible adaptation to gregarious behavior.

6. Asterocampa larvae are typically cryptic in coloration. They are green with lines and crenations of whitish yellow. In addition, larvae of the Clyton group develop longitudinal bands of whitish yellow pigmentation under the cuticle, a condition not known to me to be found in many other apaturines. This suite of markings produces a disruptive appearance rather than crypsis and might even be a mimetic or aposematic signal to some unknown predator observer.

Crypsis in enhanced in other populations of hackberry butterflies by the reduction of all light-colored body markings of the larvae. This

condition appears independently within the genus.

7. No other apaturine larvae have been reported to be gregarious feeders other than those of the Clyton group of *Asterocampa*. Gregarious hackberry butterfly larvae communicate by silk trails and touch (pers. obs.). They exhibit a feeding site cleaning behavior, active frass removal, which is considered to be a defense against potential predators and parasites which might locate the larvae by the volatile chemicals in the frass. Caterpillars have been observed to bite pellets of frass and throw them off leaves on which the larvae are feeding.

8. Apaturine pupae are not typically highly arched or irregular in outline but this condition occurs in a few genera. The pupae of *Asterocampa idyja* are slightly more arched than those of other members of the genus. A measure of this arching is the relative length of the metanotum to that of the first abdominal segment.

9. The abdominal keel is composed of the dorsal ridge of abdominal segments 3-8. Anteriorly these segments are either pointed (Clyton

group) or blunt (Celtis group).

10. The morphology of the cremaster in most apaturine pupae is typically nymphaloid in appearance. A few Apaturinae have a greatly elongated cremaster which serves to hold the pupa flush against its substrate. Asterocampa and Chitoria are the only genera to accomplish this by a highly elongate pad of hooks reaching anteriorly to the level of the sustainers. Within the hackberry butterflies only A. leilia does not have an elongate bed of cremastral hooks. The anterior area normally occupied by the cremastral hooks is replaced with short, undifferentiated setae. This condition is viewed as a modification by loss or de-differentiation, rather than a primitive condition.

11. Most apaturine butterflies have the bars in the discal cell unbroken; that is, there are only 2 bars, one somewhat centrally placed and the other placed at the end of the cell. In some Apaturinae the more basal bar is "broken" into 2 spots, the anterior half of the bar a greater or lesser distance from the origin than the posterior half. The halves evidently lie in different fields by reason of their belonging on different sides of the median vein during development of the discal cell. Only

Asterocampa celtis has a broken discal bar among the hackberry butterflies.

12. The zigzag pattern of postmedian spots found in most hackberry butterflies might be ancestral in Asterocampa. Only A. idyja has postmedian spot M2 adjacent to M3, the postmedian spots more or less form a linear band on the forewings. All the anterior foci are more basal, resulting in the correlated character of the discal bars placed very close together. It is possible that this modification was brought about by selection favoring a phenotype closer to the pattern of other sympatric subtropical butterflies. The latter might serve as models within a mimicry ring. Smyrna blomfildia (Fabr.) is one such butterfly with a pattern very much like that of A. idyja. It is a very strong flier and might serve as a model for the weaker-flighted hackberry butterfly. The relative palatabilities of these butterflies has not been tested. In the light and typical phase of A. idyja argus the band on the forewings is further modified into a thicker, solid golden band. This phenotype is even more like that of Smyrna.

Virtually all Apaturinae do not show this zigzag pattern and have postmedian spots M2 and M3 equidistant from the base of the wing. In some species, M2 is even more basal. I do not feel that out-group comparison would lead one to the right hypothesis of polarity for this character.

13-15. Various apparent reductions and other modifications of limbal spots in the FW can be considered derivations of a basic nymphaloid ground-plan with well-formed eyespots. Clyton group hackberry butterflies have lost all eyespot expression in the forewings.

I can't help but feel that the common denominator, or primitive condition, in the Apaturinae is to have only limbal spot Cu1 expressed as an eyespot. Could spots M1 and M3 become derepressed in *A. leilia* and *A. celtis antonia*? The genetics of pattern formation in hackberry butterflies would be an interesting and enlightening study.

16. The expression of limbal spot A2 as an eyespot in the HW as considered relative to the basic nymphaloid plan is primitive. It is not found at all in the Clyton group of *Asterocampa*, nor, to my knowledge, in any other Apaturinae, except members of the Celtis group.

Could hackberry butterflies be specializing evolutionarily in a form of predator avoidance as adults by derepression of eyespots, rather than by disruptive coloration (or some other such tactic)?

17. A brush of hair-scales is found dorsally on the membrane separating the male genitalia and the eighth abdominal tergite in hackberry butterflies. These are erected when the genitalia are extruded. This brush is found in many apaturine butterflies. The hair-scales are straight or curved in *Asterocampa*, but are usually straight in other Apaturinae. The anal brush of the male terminalia would appear to be apomorphic in the recurved condition (*A. celtis*).

18. The uncus in male Apaturinae is almost always pointed poster-

iorly. A few species have a bifid uncus with a narrow notch. All *Asterocampa* have a bifid uncus, but the notch is very shallow and the points very blunt in Celtis group members.

19, 20. Most apaturine butterflies (all genera have been examined) have fairly long male genitalia (lengths of saccus and aedeagus relative to length of valves). The ductus bursae of the female is similarly elongated in these butterflies. In some Apaturinae the valves are secondarily quite long (e.g., Sasakia). In Asterocampa, members of the Celtis group have relatively shorter aedeagi and sacci relative to valvi than do members of the Clyton group. Measures of these lengths can be expressed in terms of ratios of lengths. These ratios can serve to separate species of hackberry butterflies. It is not known whether or not these differences might serve as mechanical isolating factors.

The ability of different populations to interbreed is a species characteristic. Speciation may occur without this ability being impaired if some other genetically isolating mechanism is evolved. Therefore, the ability of populations to interbreed is viewed as a symplesiomorphy and, correspondingly, the inability to interbreed is a possible synapomorphy. Field and laboratory studies indicate lack of interbreeding between most species pairs of hackberry butterflies, but it is not known whether *Asterocampa idyja* can interbreed with *A. clyton*. Other pairings of *A*.

idyja would most probably be negative.

One adult character left out of the table is color phase expression. All species of hackberry butterflies have the ability through an unknown genetically mediated mechanism to express both a light and dark phenotype. The expression is carried out through what appears to be a low or high number of wing and body scales attaining darker pigmentation. Although the pathway of pigments has not been worked out in Asterocampa, there is reason to believe that non-structural pigmentation is mainly due to different or different oxidation states of [phaeo-] melanins in the wing scales, much as it appears to be in the nymphalid Precis coenia (= Junonia coenia (Hübner)) (Nijhout, 1980b). In A. clyton the dark phase has been given many names (e.g., "proserpina"). Dr. W. J. Reinthal recognized phases in A. celtis (ms.), and spring A. leilia are lighter than fall specimens. In some populations of hackberry butterflies one or the other phase seems to have been lost (see: A. idyja).

Biogeographic characters are included in the table as a comparative data set and will be discussed in the appropriate section. The pattern given here seems to reflect the morphological character distribution but

other scenarios will be explored.

Wagner network analysis (Lundberg, 1972) revealed the existence of both the Celtis and Clyton groups of hackberry butterflies (Table 9: characters 1-3, 5, 7, 9, 14, 16, 18, 19) (Figure 8, Table 10). Other character patterns confirm species differences (characters 8, 10-12, 17, 20 (both parts)). Character 4 is better interpreted as a homoplasy for host plant use between A. leilia and one population of A. celtis antonia.

"ANCESTOR"

Characters 6, 13, and 15 involve pigmentation and show convergences in states among the species. The characters 4, 6, 13, and 15 were coded accordingly for network analysis.

Hackberry butterfly species distance matrix (Manhattan Table 10. distances as computed from Table 9).

TAXA	LEILIA	CELTIS	CLYTON	IDYJA	HTU1	HTU2	"ANCESTOR"
LEILIA	_	_	_	_	_	-	_
CELTIS	5	_	-	_	_	_	_
CLYTON	15	16	_	_	_	_	_
IDYJA	18	19	3	_	_	_	_
HTU1	2	3	13	16	_	_	_
HTU2	15	16	0	3	13	_	_

11

14

11

HTU1 (with character states: 011101110111100111100) connects A. celtis (0111011101011001011110) to the interval between A. leilia (011001110011100111100) and A. idvia (100110001110011010001). HTU2 (100110011111011010000) connects A. clyton (10011001111101-1010000) to the interval between HTU1 and A. idyja.

A hypothetical ancestor (111101110111100111000) was fitted to the network, and it roots onto the interval between HTU1 and HTU2. The resulting Wagner tree is shown in Figure 9.

Hypothesizing polarities for the characters one can postulate synapomorphies with which to construct a cladogram. A cladogram of relationships among the 10 taxa of Asterocampa recognized in this revision is shown in Figure 10. The relationships between taxa are presented as a series of branching points where each furcation marks the postulated origin of monophyletic taxa. The branching pattern is documented by

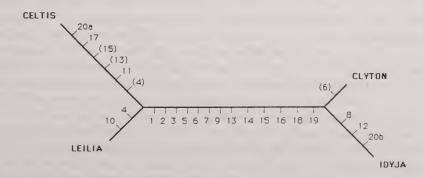


Fig. 8. Wagner network of hackberry species. Potential homoplastic characters are in parentheses.

hypothesized synapomorphies. The numbers on the cladogram correspond to those listed following the figure where argumentation for the branching pattern is given.

Wagner calculations were made on the four species of hackberry butterflies. The Wagner Network and Tree are congruent with the proposed cladogram. Additional intraspecific taxa are attached within the cladogram and discussed in the text.

The overwhelming conclusion one can draw from these dendrograms is that the Celtis group and Clyton group of hackberry butterflies are quite different from one another. The Clyton group is very well supported by characters, the Celtis group less so.

Another observation is that *Asterocampa clyton* is poorly defined by the characters examined in relation to *A. idyja*.

- 1. The out-group used in the cladogram of hackberry butterflies is all of the other apaturine genera. The possibility that *Chitoria* and *Asterocampa* are sister groups has been discussed. These 2 genera share the presumably synapomorphic characters: 1) larvae with reduced basal antler socli; 2) pupae with elongated cremastral pad; 3) male genitalia with reduced gnathos. Whether *Chitoria* is a monophyletic genus or not awaits investigation, as only the immature stages of one species, *C. ulupi* (Doherty), are known. *Asterocampa* is considered to be a monophyletic group. Members of this genus share the synapomorphy, male genitalia with bilobed uncus, and all are Nearctic in distribution.
- 2. The Celtis group is thought to be a monophyletic group. The true hackberry butterflies (proposed common name) share the following

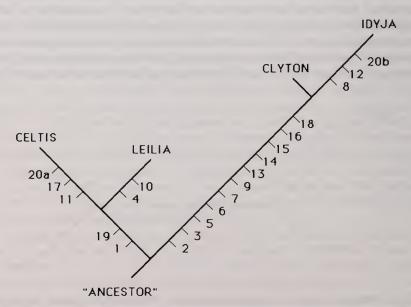


Fig. 9. Wagner tree of hackberry butterfly species.

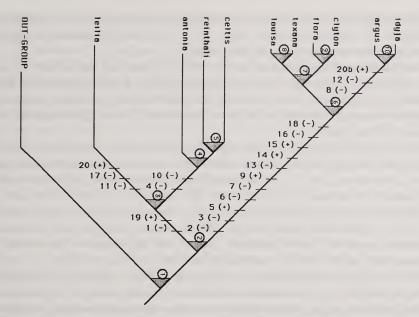


Fig. 10. Cladogram of relationships among the hackberry butterflies in relation to other Apaturinae.

probable synapomorphies: 1) eggs with wrinkled chorion between longitudinal ribs; 2) male genitalia with relatively short saccus; 3) reduction of basal antler scolus AB5. These butterflies are relatively unmodified from the hypothetical archetype, the adults having virtually all of the limbal eyespots well developed on both surfaces of both wings.

The Clyton group is the monophyletic sister group of the Celtis group of hackberry butterflies. These are distinguished by the synapomorphies: 1) eggs lacking aeropyles on lower (bottom) halves; 2) eggs deposited in tightly packed multi-layered masses; 3) larvae gregarious as early instars; 4) larvae banded; 5) adults with virtually all limbal spots in FWs not expressed as dark spots; 6) limbal spot on anal cup ventrally not expressed (HW limbal spots ventrally generally not well expressed). Other characters used to distinguish the Clyton group include: 1) segments of pupal abdominal keel anteriorly sharp; 2) male genitalia with narrowly notched uncus. This is a well-defined taxon for which the common name of American emperors is proposed.

3. Asterocampa celtis and A. leilia appear to be sister species. The 3 recognized subspecies of A. celtis share the following synapomorphies: 1) they have apparently lost the ability to interbreed with A. leilia (only A. celtis antonia tested in laboratory breeding trials); 2) the basal discal bar is divided into 2 spots (broken discal bar); 3) the male brush over the terminalia is recurved. A. leilia has the following autapomorphies: 1) sole usage of Celtis pallida as larval food plant; 2) pupal cremastral bed

of hooks shortened so that pupa does not hang flush against its retaining surface; 3) female genitalia with very short ductus bursae; 4) high temperature tolerance in all life stages.

4. The 2 more eastern subspecies of *A. celtis* are distinguishable from *A. celtis antonia* by the reduction of expression of FW limbal spots M3 and Cu1. Unlike *A. celtis celtis* and *A. celtis reinthali*, *A. celtis antonia*, in one of its populations (called here "mexicana"), uses *Celtis pallida* as

a larval food plant.

5. A. celtis celtis and A. celtis reinthali are sister subspecies (if there are such things). This eastern United States clade is distinguished by the synapomorphies: 1) virtual loss of basal antler scolus AB5 in larvae; 2) lack of expression of limbal spot M3 in FWs of adults. The latter subspecies is distinguished by: 1) large size; 2) found in peninsular Florida; 3) limbal eyespot M1 of HW asymmetrically drawn out into point; 4) pupil of limbal eyespot Cu1 of FW lateralized. The latter 2 characters might well be correlates of large adult body size.

6. Asterocampa clyton and A. idyja are sister species. A. clyton is characterized by its presumed inability (virtually allopatric) to interbreed with A. idyja, but otherwise retains the hypothetical primitive character set of the Clyton group. Asterocampa idyja has the autoapomorphies: 1) larva with darkly pigmented anal horns (not always expressed); 2) pupa with relatively short metanotum as measured dorsolongitudinally; 3) postmedian spots in anterior portion of the wing closer to discal cell than in other hackberry butterflies. It is also characterized by having a relatively long aedeagus and saccus in the male (genitalia).

7. The 2 more eastern subspecies of *A. clyton* are more similar to each other than either is to either of the 2 more western subspecies, based on pigmentation of larvae and adults. The antlers of caterpillars of *A. clyton clyton* and *A. clyton flora* are relatively shorter than those of *A. clyton texana* and *A. clyton louisa*. FW limbal spot Cu1 is virtually never even partially expressed in the 2 more eastern subspecies.

8. A. clyton texana and A. clyton louisa are presumably sister subspecies. These subspecies have no readily apparent synapomorphies, but A. clyton louisa has many character differences from A. clyton texana (= "subpallida"), the polarities of which are unknown (e.g., larval and adult pigmentation, geographic range). A. clyton louisa inhabits the same geographic area as A. celtis antonia form "mexicana."

9. A. clyton clyton and A. clyton flora are sister subspecies, just as A. celtis celtis and A. celtis reinthali are, respectively. A. clyton flora is characterized by: 1) large size; 2) found in peninsular Florida; 3) virtually lacking individuals expressing dark phase phenotypes.

10. Asterocampa idyja is composed of 2 phenotypically rather different subspecies. The nominate subspecies is found in the Greater Antilles, a geographic character considered here to be autapomorphic. A. idyja argus has a banded form which is involved in a Neotropical

mimicry complex. The unbanded form is quite similar to *A. idyja idyja*, but is not nearly as pale.

It is informed conjecture to say that *Asterocampa leilia* speciated from the *A. celtis* line by largely allopatric adaptation to its present host plant. The ancestral *A. celtis*, remaining on the tree-like hosts like all the other hackberry butterflies, would then lose the solid basal discal bar in the wings for some obscure reason. It is interesting to note that the phenotypically primitive *A. celtis antonia* (form "mexicana") uses *Celtis pallida* as a larval host together with the tree-like hackberry species. Perhaps colonization of spiny hackberry represents a space into which *A. celtis* populations can speciate.

In the opinion of this author, the inclusion of A. leilia with A. celtis to form a species group is justified on phenotypic and ecological grounds, although it is not well supported by cladistic argumentation.

The problem with hypothesizing a clade for taxa below the species level is that there is presumably the ability of such taxa to exchange genetic information with conspecifics, thus affecting the relative "possession" of apomorphic characters. Characters are often maintained as polymorphisms in such populations and rarely become fixed. With such possibilities of interchange even fixed characters are liable to become polymorphic again. For these reasons taxonomy based strictly on clades below the species level should be done cautiously if at all (see also: Baum and Estabrook, 1978). Such clades as are presented here rest largely on the improbability of genetic exchange between largely allopatric populations containing relatively sedentary individuals. Classification based on these clades freezes this moment in their evolutionary time. It is not unreasonable to suppose that both Floridian subspecies of A. celtis and A. clyton, respectively, will gradually intergrade with and merge into their respective nominate subspecies, barring a near future re-isolation.

### BIOGEOGRAPHY:

The distribution of hackberry butterflies can be given evolutionary explanation with the application of techniques of historical biogeography (Cracraft, 1975). Before the emergence of vicariance biogeography as an acceptable explanation for distributions of some organisms, continental drift was a source of controversy with regard to butterflies of North America (Eliot, 1946; Forbes, 1947). North America does not seem to have an endemic family to butterflies, unless it is the Papilionidae (Hancock, 1983). All the New World family-level groups can theoretically be derived from ancestral Old World forms (Smart, 1979) via the Bering Strait or West African/Eastern South American connections existing before the total break-up of Gondwanaland. The few relict groups (recognized as such) of butterflies in the New World are confined to mountains and islands.

The distribution of temperate and subtropical Nearctic butterflies has

been a source for biogeographic speculation, often without the aid of scientific methodology, which has given rise to a few precepts:

- 1. Glacial maxima with coordinate changes in American climate and vegetation zones (Delcourt and Delcourt, 1981) must have pushed butterflies into refugia (Brown, 1981; Klots, 1965). Recolonization of temperate North America is occurring today, at different rates for different butterflies. This colonization includes butterflies mostly of Neotropical origin.
- 2. Only certain butterfly groups have widely dispersing females that are good enough colonists to cross mountain or water barriers. To account for the wide distribution of other butterflies, their females must have had easier routes of colonization, either by land- (or host plant-) bridge or by land connection of close proximity which no longer exist today (vicariance is highly probable for some).

3. Isolation and allopatric speciation account for most of the taxonomic diversity observed in butterflies. Subsequent sympatry of closely related butterflies is a recent event owing to changes in climate, habitat and distribution of host plants.

Looking again at the cladogram generated for hackberry butterflies and replacing the taxa with the geographic areas they inhabit (Figs. 11, 12), there are patterns of distribution that could be assigned to either dispersal or, alternatively, vicariance events. These patterns are discussed by number, corresponding with the clades in the first figure.

1. The first noticeable feature of the graph is that *Asterocampa* is found in North and Central America but is most closely related to Old World genera, specifically to *Chitoria* which inhabits eastern Asia (ne. India, se. Asia, central China, Formosa). What little there is known about such a pattern of distribution would indicate that the most attractive explanation for the New World location of hackberry butterflies is a warm-climate, pre-Miocene (Arcto-Tertiary) dispersal of butterflies from eastern Asia to North America by way of the Bering Land Bridge. Subsequent isolation and adaptation may have given rise to *Asterocampa*.

There are a few tenuous lines of evidence that strengthen the argument for such an occurrence. The first question that might be asked concerning the probability of *Asterocampa* also having been part of an Arcto-Tertiary exchange is: Is there evidence of a continental interchange of other organisms and, if so, when did it or they occur?

Looking at the present distribution of organisms there are many species- and genus-level taxa that are found only in eastern Asia and in similar climates in North America. An example would be plant members of the Notophyllous Broad-leaved Evergreen forest (Wolfe, 1979), such as *Liquidambar*. The gall- and lerp-forming psyllids of the genus *Pachypsylla* (also associated with *Celtis*) are among the insect examples. They are distributed on hackberry in both North America and in Japan (Hodkinson, 1980).

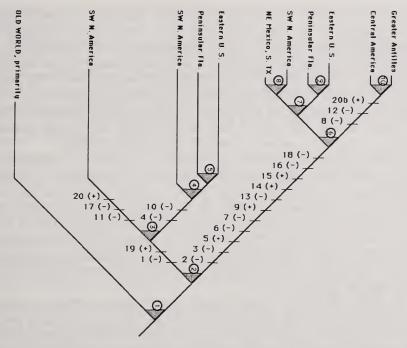


Fig. 11. Area cladogram of relationships among the hackberry butterflies in relation to other Apaturinae.

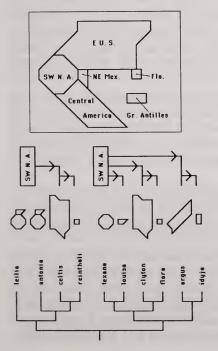


Fig. 12. Hypothesized biogeographical patterns shown by current distributions of hackberry butterflies.

Land connections permitting such biotic transfers occurred many times during the Tertiary (Hopkins, 1959). The Eocene/Oligocene is theoretically more attractive than the Miocene for the interchange of subtropical to temperate terrestrial organisms based on the climatic inferences of the floristic evidence (Wolfe and Leopold, 1967). The latter time period was evidently too cold to support appropriate flora. The Middle Eocene flora from the Gulf of Alaska contains members of the Ulmaceae having drip tips on their leaves (Wolfe, 1977) such as those which are found on leaves in present day tropical forests.

2. The primary division in the genus *Asterocampa* is one of oviposition strategy/host plant utilization and probably is not geographic. Females of the Clyton group deposit large clutches of eggs on the host and the early instar larvae feed gregariously. Oviposition is largely confined to mature trees with large leaves and while the larvae grow better on new growth of the host plant. They are able by eating together to consume old growth as well. These butterflies are more often found in old stands of their host plants which normally occur along rivers than those of the other species group.

Females of the Celtis group deposit small numbers of eggs on their hosts and the larvae feed more or less singly. Only new growth of the host is available to early instar larvae even in *A. leilia* which has first instar larvae with very well developed mandibles. Oviposition occurs on the growing points of hosts usually on seedlings or the lower branches of young trees. Oviposition in *A. leilia* is on the growing points of the host bushes. Perhaps as a consequence of being more tissue specific (confined?), these butterflies are better colonists of their hosts and are wider ranging. They are not only confined to river systems, but are also able to find isolated stands of the host plant, much as the snout butterflies (Libytheidae: *Libytheana*) do. Snout butterflies also feed on the new growth of hackberry.

The 2 species groups occupy roughly the same geographic areas, with the exception of the expansion southeastward of the A. idyja into the Neotropics (6). It is a common occurrence to find one member of each species group in a given locality and thus the various forms occur in geographic pairs (e.g., A. c. antonia and A. c. texana + A. c. louisa, A. c. reinthali and A. c. flora).

3. A. leilia appears to have invaded the more arid habitat of its host permitting the butterfly to occur at lower local elevations and over broader areas than the other grossly sympatric hackberry butterflies in southwestern North America.

4 and 7. The A. celtis and A. clyton lines seem to have expanded eastward leaving A. c. reinthali and A. c. flora as Pleistocene relicts in peninsular Florida (5 and 9). Some differentiation of A. c. antonia has occurred in northeastern Mexico where the females are smaller than average and have decreased expression of FW limbal spots (form "mexicana"). In this same area A. clyton texana has apparently differ-

entiated into A. clyton louisa which has darkened antennae and FW apices (8).

10. The distribution of *A. idyja* is particularly interesting: one subspecies occurs in the Greater Antilles and the other in Central America. Its Caribbean host plant occurs in Central America as well. It appears to be the lesser complicated explanation that the island populations are derived from the mainland. The closest relative of *A. idyja* occurs in the southwestern parts of North America adjacent to the present distribution of *A. idyja argus*.

There are a number of hypotheses relating the major Caribbean islands and organisms to Central America (Alain, 1958; Baie, 1970; Comstock and Huntington, 1949; Freeland and Dietz, 1971; Khudoleg and Meyerhoff, 1971; Pregill, 1981; Rosen, 1975; Scott, 1972; Shields and Dvorak, 1979; Trelease, 1918). The first and most often cited hypothesis holds that migrant females colonized the islands from the mainland at a time when the configuration of land masses was as it is now (large scale dispersal). Related hypotheses are similar but include either a different configuration of land masses or, through sea level changes, differing boundaries to existing land masses (short scale dispersal and/or vicariance). The difficulties in differentiating between vicariance and dispersal events are virtually insurmountable if both are equally likely in the ignorance of the timing of such events (see also: Howden, 1974). An extreme hypothesis (large scale vicariance) would envision a single land mass inhabited by A. idyja which subsequently split into 2 regions of which one is contiguous or equivalent to Central America and the other to the Greater Antilles.

Because *A. idyja* is a relatively poor colonist I do not favor large scale dispersal as the most likely event leading to its colonization of the Greater Antilles. It also seems unlikely that the species is old enough (stasis would have to characterize the evolution of morphological characters in this species!) to have participated in a large scale vicariance event even if one did occur (Pregill, 1981). A short dispersal from the Yucatan peninsula at a time when Cuba was effectively closer to that part of Mexico is to me the most likely way in which *A. idyja* got to the islands. This could have been achieved when a drop in sea level occurred.

The timing of this hypothetical event is another matter. There is no morphological evidence which might support early versus late dispersal or vice versa. The island subspecies does not exhibit the presumed mimetic morph (light phase individuals). This could be due to a founder effect, a result of sampling fixation of a pre-existing polymorphism, or just owing to the morph occurring at such a low frequency that it has not yet been collected. This low frequency might be attributable to a lower relative fitness of the mimetic morph in the island environment without its presumed model (and selection agent?) being present.

The possibility of A. celtis occurring in Cuba (Lucas, 1857) is intri-

guing. This species, with its better dispersal capabilities than members of the Clyton group, would more likely be a colonist from Florida than Central America. The probability of a form occurring in the Greater Antilles being related to the Floridian *A. celtis reinthali* is therefore higher, I think, than this from being related to *A. celtis antonia*. If this theoretical butterfly were related to the latter, one would have support for a generalized track for hackberry butterflies from Central America to the Greater Antilles.

Figure 13 is given as a summary of hypothesized events in the evolution of *Asterocampa*.

## **Conclusions**

Asterocampa Röber is better known as a result of this revision. This work has advanced the understanding of hackberry butterflies with regard to their taxonomic history, morphological and behavior characteristics, and relationships one to another and to other apaturine nymphaloid butterflies.

The application of Fabrician names to hackberry butterflies is terminated. Asterocampa celtis reinthali is described from peninsular Florida because this butterfly population is distinct from A. alicia, here considered a subjective synonym of A. celtis celtis. Three other taxa, Asterocampa montis, A. leilia cocles, and A. subpallida are synonymized with A. celtis antonia, A. leilia, and A. clyton texana, respectively. Ten different populations of hackberry butterflies are considered worthy of valid names at this time.

Four species groupings were hypothesized after observation of butterflies in the field and in trial breeding experiments in the laboratory. These observations were supported by zoogeographic (Bowden, 1976) and morphological differences in virtually all life stages observed. The assignment of many taxa to subspecific rank represents a reduction in rank from the classification of Miller and Brown (1983).



Fig. 13. Hypothesized Evolution in Asterocampa.

A table is presented which summarizes hackberry butterfly classification proposed in this revision (Table 11).

One population of hackberry butterflies was identified as being characterizable but not considered worthy of subspecific status. This population is designated as form "mexicana" of *A. celtis antonia*. It occurs in the lower Rio Grande Valley of Texas and in northeastern Mexico and is largely sympatric with *A. clyton louisa*.

Asterocampa is considered to be completely host specific on hackberry (Celtis).  $A.\ leilia$  is host specific on  $Celtis\ pallida$ . Other species use a variety of other species of hackberry as larval host plants, but only exceptionally do they use  $C.\ pallida$  (one population of  $A.\ celtis\ antonia$ ).

Table 11. Summary classification of hackberry butterflies and suggested common names.

Hackberry Butterflies Asterocampa [Celtis group] true Hackberry Butterflies [the] Hackberry Butterfly 1. celtis [Eastern] Hackberry Butterfly a. celtis Florida Hackberry Butterfly b. reinthali Western Hackberry Butterfly c. antonia Desert Hackberry Butterfly 2. leilia American Emperor Butterflies [Clyton group] Tawny Emperor 3. clyton Tawny Emperor a. clyton Florida Emperor b. flora c. texana Pale Emperor [Rio Grande] Valley Emperor d. louisa **Dusky Emperor** 4. idyja a. idyja Dusky Emperor b. argus Banded Emperor

Keys and descriptions of all these taxa are presented in this revision. Biological characteristics of each species are discussed. Distribution maps and illustrations of all adult and most immature stages are given in plates. Developmental studies of wing pattern development are still needed to support suggestions of adult morphological evolution made here. The ability to describe wing pattern and color in terms of developmental foci and fields was very useful.

Cladistic methodology was used to hypothesize phylogenetic relationships among members of the genus Asterocampa and closely related genera. Asterocampa is considered to share a recent common ancestry with the eastern Palearctic genus Chitoria.

Two distinct groupings of hackberry butterflies emerged, based on synapomorphic characters associated with 2 different life history

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strategies found in the genus. These were assigned species group status, until the monophyly of the Celtis group is better analyzed.

Asterocampa is found to be Nearctic in distribution. *Doxocopa*, which is a Neotropical genus with some members in North America, is quite different from *Asterocampa* morphologically. It probably had a different route of introduction into the New World than is proposed for *Asterocampa*.

Biogeographical interpretation of the phylogenetic pattern for hackberry butterflies developed through cladistic methodology yielded several hypotheses. Populations of hackberry butterflies in the eastern United States are seen to be derived from those of the Southwest. A. celtis reinthali and A. clyton flora were thought to have evolved through recent (not remote past) isolation in peninsular Florida. A. idyja idyja's arrival in the Greater Antilles is hypothesized to be from a population of butterflies occurring in Central America at a time when such dispersal would have been much more favorable than it is today. It probably was also a fairly recent event.

The number of characters necessary by cladistic methodology to track recent evolution in the genus were not found, leaving classification below the species level unresolved by this method.

Traditional application of the biological species concept in conjunction with studies of interpopulation sympatry and morphological character state distribution helped in making decisions of which populations should be accorded subspecific and which specific status. There are still problems with classification at this level within the genus. These might better be addressed through quantitative genetics studies.

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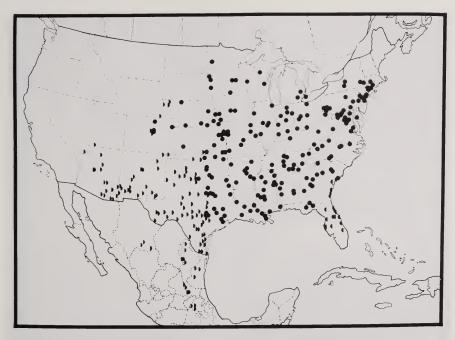


Plate 1. Geographic distribution of Asterocampa celtis: ● A. celtis celtis, ◀ A. celtis reinthali, ▶ A celtis antonia.



Plate 2. Geographic distribution of Asterocampa leilia.



Plate 3. Geographic distribution of Asterocampa clyton: ● A. clyton clyton, ● A. clyton flora, ● A. clyton texana, ● A. clyton louisa.



Plate 4. Geographic distribution of *Asterocampa idyja: A. idyja idyja, A. idyja argus.* 

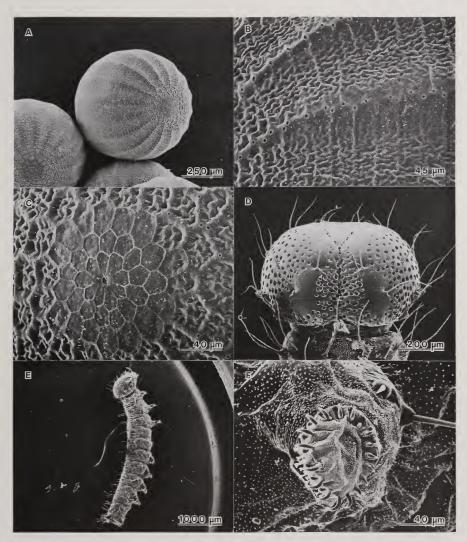


Plate 5. A. celtis celtis: A) E (top), Ontario, Canada; B) E (side, detail; C) E (micropyle). A. celtis antonia: D) L1 (top, head-note unbranched setae), TX; E) L1 (right side); F) L1 (bottom, proleg-note crampets). E = Egg
L1-L5 = First - Fifth Instar Larvae
P = Pupa

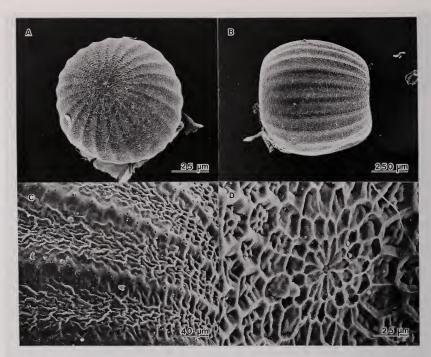


Plate 6. A. celtis antonia: **A**) E (top), AZ; **B**) E (side), TX; **C**) E (side, detail), TX; **D**) E (micropyle), TX.

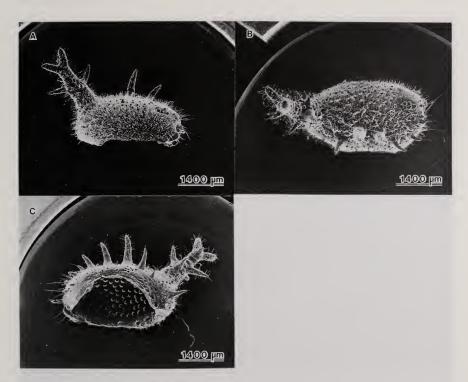


Plate 7. A. celtis antonia: A) L5 (front, left part of head capsule), TX; B) L5 (side, right part); C) L5 (back, left part).

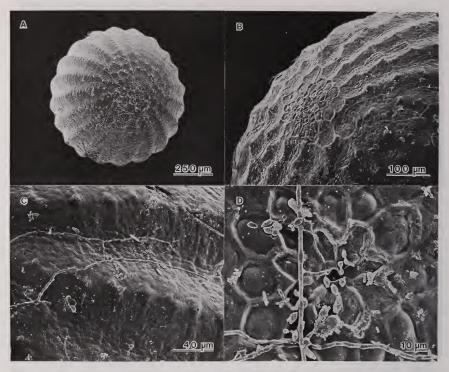


Plate 8. *A leilia:* **A**) E (top), AZ; **B**) E (micropylar region); **C**) E (side, detail); **D**) E (micropyle).

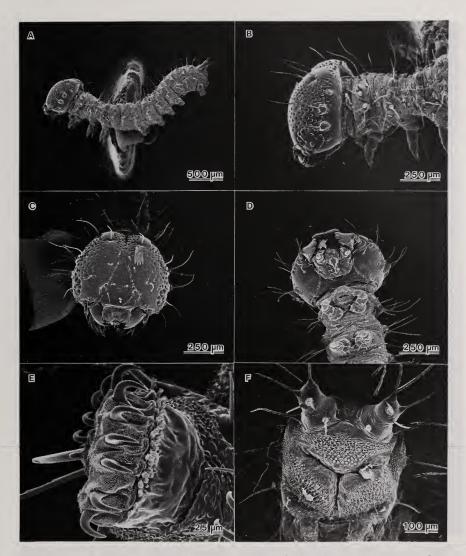


Plate 9. A. leilia: A) L1 (left side), AZ; B) L1 (left side, head and thorax); C) L1 (front, head); D) L1 (bottom, head and prothorax-note toothed mandibles and neck gland; E) L1 (bottom, proleg-note crampets); F) L1 (rear, anal segment).

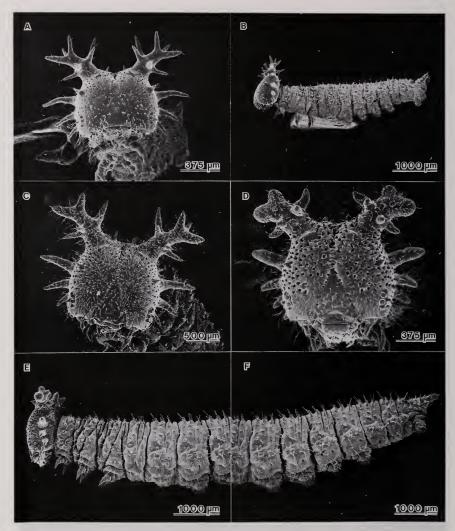


Plate 10. A. leilia: A) L2 (front, head), AZ; B) L2 (left side), AZ) C) L3 (front, head), TX; D) diapause L3 (front, head-note stubby antlers), AZ; E and F) diapause L3 (left side-note that abdominal segments 2-4 are duplicated in this composite figure), AZ.

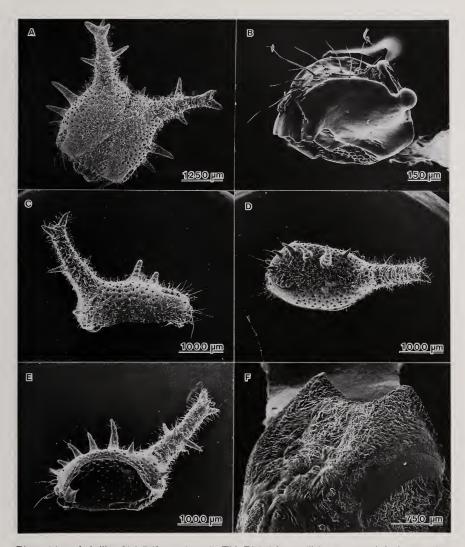


Plate 11. A. leilia: A) L5 (front, head), TX; B) L5 (mandible-note undulating cutting edge at lower left), AZ; C) L5 (front, left part of head capsule), AZ; D) L5 (side, right part); E) L5 (back, left part); F) P (left side and front, head), TX.

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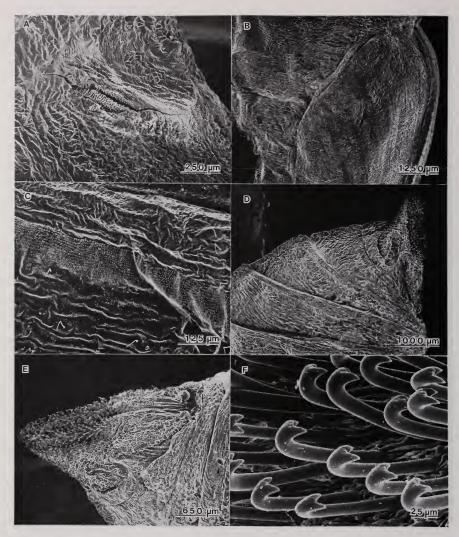


Plate 12. A. leillia: A) P (side, thoracic spiracular opening), TX; B) P (left side, middle segments); C) P (left side, abdominal segments-note bent setae and microfile on posterior edge of segment); D) P (left side, posterior segments; E) P (left side and bottom, cremaster-note shortened bed of hooks); F) P (bottom, cremastral hooks).

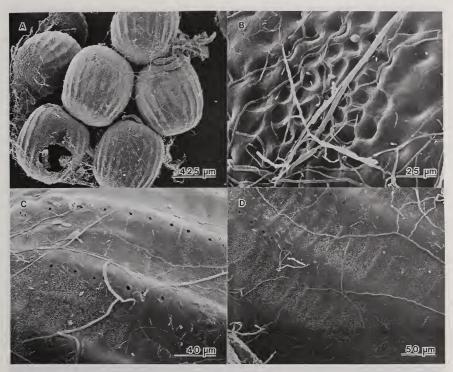


Plate 13. A. clyton clyton: A) E (side-note scelionid emergence hole), VA; B) E (micropyle); C) E (side near top); D) E (side nearer bottom).

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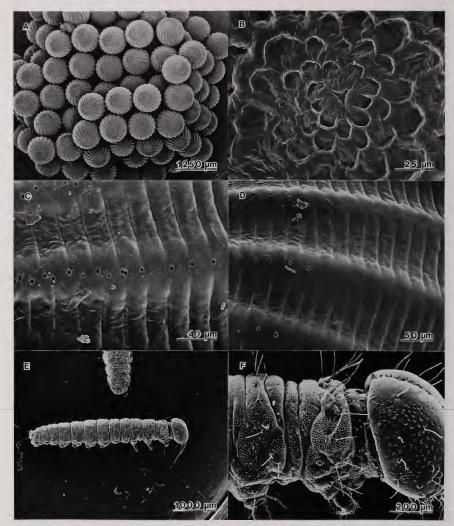


Plate 14. A. clyton texana: **A**) E cluster (top), AZ; **B**) E (micropyle); **C**) E (side near top); **D**) E (side nearer bottom); **E**) L1 (right side), TX; **F**) L1 (right side, head and prothorax).



Plate 15.\* A. clyton louisa: A) L5 (front, right part of head capsule), TX; B) L5 (back, right part); C) L5 (side, left part).

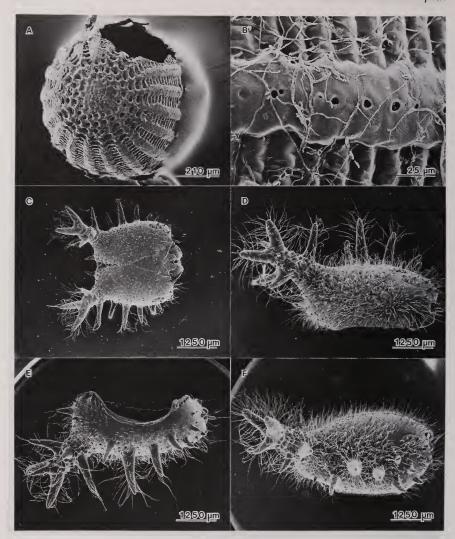


Plate 16. A. idyja argus: A) E (top-note scelionid emergence hole), Oaxaca, Mexico; B) E (side, detail); C) L4 (front, head capsule), Oaxaca, Mexico; D) L5 (front, left part of head capsule), Oaxaca, Mexico; E) L5 (back, left part); F) L5 (side, right part).

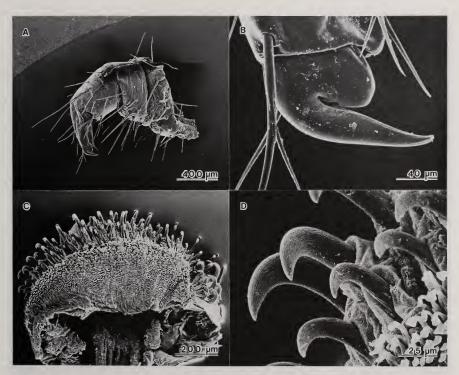


Plate 17. A. idyja argus: A) L5 (thoracic leg), Oaxaca, Mexico; B) L5 (thoracic leg, detail of claw); C) L5 (mesal side, larval proleg-note crampets and crochets), Oaxaca, Mexico; D) L5 (mesal side, larval proleg, detail).

- Plate 18. A) A. celtis antonia eggs on C. laevigata, TX-note ripening rings.
  - B) A. leilia eggs on C. pallida, AZ.
  - C) A. clyton louisa eggs mass on C. laevigata, TX.
  - D) A. clyton clyton egg mass on C. occidentalis, VA-note scelionid wasps.
  - E) A. celtis antonia diapause phase third instar larva, TX-lab reared.
  - F) A. celtis antonia fourth instar larva on C. reticulata, AZ.
  - G) A. leilia first instar larvae on C. pallida, AZ.
  - H) A. clyton clyton diapause phase third instar larvae, FL.
  - A. clyton clyton post-diapause third instar larva on C. laevigata, TX. I)
  - J) A clyton louisa second and third instar larvae on C. laevigata, TX.
  - K) A. celtis celtis fifth instar larva on C. occidentalis, VA.
  - L) A. celtis celtis fifth instar larva on C. laevigata, TX.
  - M) A. celtis antonia fifth instar larva on C. reticulata, TX.
  - N) A. celtis antonia fifth instar larva on C. laevigata, TX.
  - O) A. leilia fifth instar larva on C. pallida, AZ.

- Plate 19. A) A. clyton clyton fifth instar larva on C. occidentalis, SE United States.
  - B) A. clyton clyton fifth instar larva on C. tenuifolia MI.
  - C) A. clyton texana fifth instar larva on C. laevigata, TX.
  - D) A. clyton texana fifth instar larva on C. reticulata, AZ.
  - E) A. clyton louisa fifth instar larva on C. laevigata, TX.
  - F) A. idyja argus fifth instar larvae on C. caudata, Oaxaca, Mexico.
  - G) A. celtis celtis pupa on C. laevigata, TX.

  - H) A. celtis antonia pupal case on C. reticulata, TX.
  - I) A. leilia pupa on C. pallida, AZ.
  - J) A. leilia pupa, TX.
  - K) A. clyton texana pupa, TX.
  - L) A. idyja argus pupa on C. caudata, Oaxaca, Mexico-diseased.
  - M) A. celtis antonia, female resting on C. reticulata, TX-dorsal basking.
  - N) A. celtis antonia, female resting on C. reticulata, TX-newly emerged.
  - O) A. clyton louisa, female resting on Ulmus sp., TX.



- Plate 20. A. celtis celtis: **A** and **B**) male (dorsal and ventral), GA-reared; **C**) female (dorsal), GA-reared.
  - A. celtis reinthali: **D** and **E**) male (dorsal and ventral), FL-holotype; **F**) female (dorsal), FL-allotype.
  - A. celtis antonia: **G** and **H**) male (dorsal and ventral), N TX; **I**) female (dorsal), N TX.
  - A. celtis antonia: **J** and **K**) male (dorsal and ventral), AZ-reared; **L**) female (dorsal), AZ-reared.
  - A. celtis antonia: **M** and **N**) male (dorsal and ventral), S TX-reared; **O**) female (dorsal), S TX-reared.



- Plate 21. A leilia: **A** and **B**) male (dorsal and ventral), AZ-reared; **C**) female (dorsal), AZ-reared.
  - A. clyton clyton: **D** and **E**) male (dorsal and ventral), PA-reared; **F**) female (dorsal), PA-reared.
  - A. clyton clyton: **G** and **H**) male (dorsal and ventral), VA-reared; **I**) female (dorsal), MI-dark form, reared.
  - A. clyton flora: **J** and **K**) male (dorsal and ventral), FL-reared; **L**) female (dorsal), FL.
  - A. clyton texana: **M** and **N**) male (dorsal and ventral), TX-reared; **O**) female (dorsal), TX.



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Plate 22. A clyton texana: **A** and **B**) male (dorsal and ventral), AZ-reared; **C**) female (dorsal), AZ-reared.

A. clyton louisa: **D** and **E**) male (dorsal and ventral), Nuevo Leon, Mexico; **F**) female (dorsal), TX-reared.

A. idyja idyja: **G** and **H**) male (dorsal and ventral), Cuba; **I**) female (dorsal), Cuba.

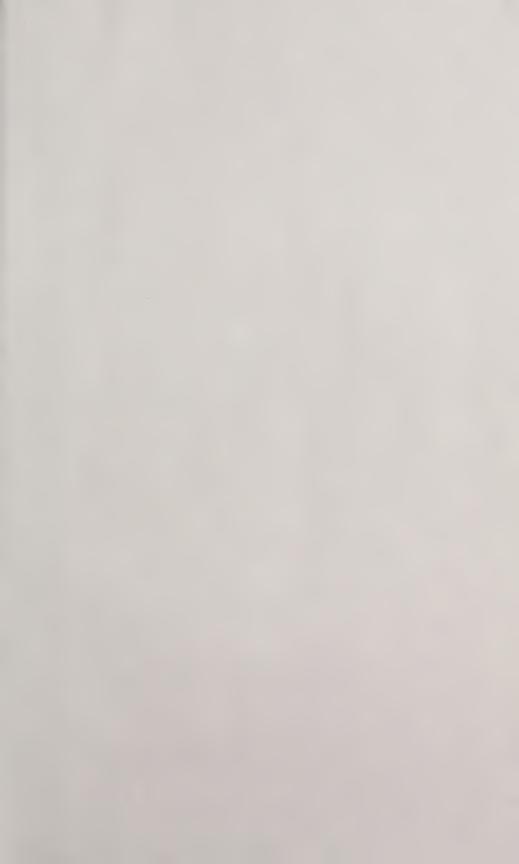
A. idyja argus: J and K) male (dorsal and ventral), Sonora, Mexico-light phase; L) female (dorsal), Veracruz, Mexico-light phase.

A. idyja argus: M and N) male (dorsal and ventral), Oaxaca, Mexico-dark phase; O) female (dorsal), Veracruz, Mexico-dark phase.











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